Multiple facets of biodiversity:

Assembly processes, trait composition, and functionality along tropical elevation gradients

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Yvonne Christin Tiede

aus Gifhorn

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Land of the Sun! Where joyous green-robes Spring
And leaf-crowned Summer deck the Earth for ever;
No Winter stern their sweet embrace to sever
And numb to silence every living thing,
But bird and insect ever on the wing,
Flitting ,mid forest glades and tangled bowers,
While the life-giving orb's effulgent beams
Through all the circling year call forth the flowers.
Here graceful palms, here luscious fruits have birth;
The fragrant coffee, life-sustaining rice,
Sweet canes, and wondrous gums, and odorous spice;
While Flora`s choicest treasures crowd the teeming earth.
Beside each cot the golden Orange stands,
And broad-leaved Plantain, pride of Tropic lands.

Alfred R. Wallace

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Chapter 1

General introduction

"We'll never succeed in global transformation unless we achieve a mindshift reconnecting mankind to biosphere." Johan Rockström

Biodiversity as the backbone for ecosystem functioning

Biodiversity encompasses biological variation at the level of genes, species, and ecosystems (Swenson 2011). This diversity is essential for the long-term resilience of ecosystems and the functioning of ecosystem processes (Oliver et al. 2015, Soliveres et al. 2016). The uneven distribution of biodiversity across the globe – especially the pattern of decreasing biodiversity from the tropics towards the poles – has fascinated ecologists since centuries (Darwin 1859, Wallace 1878). Moreover, it opened an ongoing and intense debate on the drivers of diversity patterns, e.g. evolutionary time, geographic area, temperature, productivity, metabolic rates, and biotic interactions (Allen et al. 2002, Willig et al. 2003). However, there is still no consensus on the main mechanisms behind the biodiversity patterns (Gaston 2000, Allen et al. 2003, Storch 2003).

Species are one of the fundamental units of biodiversity and taxonomic diversity provides the basis for ecosystem processes and the functioning of ecosystems. However, taxonomic diversity *per se* is a comparatively poor predictor of ecosystem functioning (Cadotte et al. 2011, Naeem et al. 2012). Rather, taxonomic diversity in concert with the phylogenetic diversity (phylodiversity) among species as well as the functional diversity of their traits affect the functioning of ecosystems (Díaz and Cabido 2001, Cadotte et al. 2009a, Flynn et al. 2011). High phylodiversity within assemblages or ecosystems can indicate the occurrence of diverse ecological strategies, indicating persistence and stability under changing environmental conditions (Forest et al. 2007, Cavender-Bares et al. 2009). Functional diversity is a measure of the diversity of functionally important traits of species or assemblages. These so-called functional traits can comprise morphological, physiological, behavioral, and phenological features that can affect the fitness of individuals (Violle et al. 2007, Mlambo 2014), the response of species to environmental conditions, and the effects of species on ecosystem processes (Petchey and Gaston 2006, Violle et al. 2007). However, relationships between the taxonomic, phylogenetic, and functional diversity of assemblages and especially their effects on ecosystem processes are complex and still not fully resolved (Schwartz et al. 2000, Arnan et al. 2017).

Irrespective of the knowledge gaps regarding related patterns and processes, biodiversity faces a worldwide and immense loss, which additionally fuels the current biodiversity research. Among the main drivers for the loss of biodiversity are anthropogenic climate change and the destruction, fragmentation, alteration, and disturbance of habitats (Brook et al. 2008, Asner et al. 2010). Decreasing biodiversity generally comprises a loss of species and therefore of taxonomic diversity which almost always involves the loss of phylogenetic diversity and functional diversity, all of which are expected to affect the stability and functioning of ecosystems (Chapin III et al. 2000, Olden et al. 2004, Soliveres et al. 2016). The ongoing loss of biodiversity may, therefore, be as significant in its impact on ecosystem functioning as other global change stressors that have already received substantial political attention (Houghton et al. 1990, Intergovernmental Panel on Climate Change 2007).

Considering the rapid loss of biodiversity worldwide, it will not be possible to simultaneously preserve all components of biodiversity (Zupan et al. 2014, Arnan et al. 2017). This leads conservation into a dilemma because the traditional conservation approach that aims to preserve high levels of taxonomic diversity does not necessarily lead to an equal preservation of phylodiversity and functional diversity (Devictor et al. 2010). However, effective conservation management should focus not only on taxonomic diversity but also on ecosystem properties and ecosystem functions. Therefore, a comprehensive understanding of the processes that drive patterns of biodiversity and of the relationships between taxonomic, phylogenetic, and functional diversity and ecosystem functioning is urgently required. Biodiversity research that aims to understand changes in biodiversity and its components along gradients of changing environmental conditions therefore is a centerpiece of ecology and conservation (Hannah et al. 2002, Hooper et al. 2005, Chazdon et al. 2009, Fayle et al. 2015).

Why elevational gradients matter

Environmental gradients provide a practical basis for studies that seek to understand the relationships between changing environmental conditions, biodiversity, and ecosystem processes. One of the most striking biodiversity patterns is the decline of taxonomic richness with decreasing temperature, both with increasing latitude and with increasing elevation (Bergmann 1847, Gaston 2000, Ricklefs 2004). The vertical zonation of mountain habitats recapitulates the progression of habitats and environmental conditions from the equator to the poles in a tiny fraction of the spatial distance. Elevational gradients are therefore excellent natural laboratories for biodiversity patterns and species adaptations and can be used as model system for global patterns (Botes et al. 2006, Graham et al. 2014). Especially the absence of different geological histories along elevational in contrast to latitudinal gradients can help to draw general conclusions from biodiversity patterns (Graham et al. 2014).

Moreover, mountain ecosystems are of significant importance for the provisioning of globally important ecosystem functions (Basset et al. 2012, Edwards et al. 2014), with tropical ecosystems being of particular importance. Tropical mountain rainforests harbor especially high amounts of the global biodiversity and, at the same time, face the highest loss of biodiversity worldwide (Asner et al. 2010), making them one of the major hotspots of biodiversity (Myers et al. 2000). One of the most prominent direct threats for the biodiversity of tropical mountain rainforests is the conversion of forests into agricultural or silvicultural lands (Foley et al. 2005). Apart from such directly visible threats, also less apparent impacts from climate change affect mountain ecosystems (Asner et al. 2010). For example, global warming has already led to shifts in the distribution of a range of taxa, e.g. butterflies, grasshoppers, beetles, birds, and mammals (Walther et al. 2002, Root et al. 2003, Chen et al. 2011). The poleward migration of taxa averages 17 kilometers per decade, whereas species on mountainsides move upslope by 11 meters per decade (Chen et al. 2009, 2011). The proximity of habitats and quick temperature changes along elevational gradients may facilitate species to track their preferred thermal niche compared to latitudinal range shifts (Graham et al. 2014). Thus, upward shifts in species distributions could be detected sooner along elevational gradients than north- or southward shifts along latitudinal gradients. Elevational gradients can therefore also be used to study ecological responses to climate change (Graham et al. 2014, La Sorte et al. 2014). However, as mountain ranges do not perfectly represent climatic changes at global scales, translations of conclusions from elevational gradients to global scales should be drawn with caution (Halbritter et al. 2013, Graham et al. 2014). Altogether, the complexity and heterogeneity of mountain forest ecosystems along elevational gradients make them useful for studies of effects of abiotic and biotic factors on the taxonomic, phylogenetic, and functional components of biodiversity, as well as on ecosystem processes (Körner 2000, Qian and Ricklefs 2016).

The three components of biodiversity

Taxonomic diversity – biological richness at the species-level

Traditionally, patterns of biodiversity have been described and explained at the taxonomic level, e.g. in numbers of species. Indeed, much of our current understanding of biodiversity patterns mainly is derived from analyses of patterns of species richness and species turnover along environmental gradients (Pausas and Austin 2001, Buckley and Jetz 2008). The decreasing taxonomic diversity from the equator to the poles and with increasing elevation is certainly among the most striking patterns in ecology. One of the main drivers of this pattern is the decreasing temperature with increasing latitude and elevation, due to its negative influence on growth and metabolic rates of plants and animals (Allen et al. 2002, Brown et al. 2004). Also, net primary productivity has been invoked as an important driver of taxonomic diversity (Allen et al. 2007, Grace et al. 2016). However, relationships between temperature, net productivity, and precipitation make it difficult to come to general conclusions (Gaston 2000). Moreover, along elevational gradients, the species richness pattern often shows a mid-elevation peak and here again, several factors are likely to contribute to it. For example dry conditions at low elevations, cold, wet or cloudy conditions at high elevations, mountaintop extinctions during glacial minima, dispersal limitations, and geometric constraints due to an increasing overlap of species range between highest and lowest elevations can compli-

cate gradients of species richness (McCain 2007, Acharya et al. 2011, Graham et al. 2014, Longino et al. 2014, Colwell et al. 2016). Even though new approaches and more integrative models still improve our understanding of relationships between taxonomic diversity and environmental factors, the exact mechanisms behind global and regional patterns of species richness are still not completely understood (Grace et al. 2016, Colwell et al. 2016, Tang et al. 2016, Beck et al. 2017, Pontarp and Wiens 2017).

The ability to explain a substantial portion of the variation in taxonomic diversity is tremendously important for potential conservation applications and is still the most important variable for decision-making on protected areas (Veach et al. 2017). One of the reasons is the positive impact of taxonomic diversity on ecosystem processes, such as biomass production, nutrient cycling, and decomposition (Tilman et al. 2006, Cardinale et al. 2011, Soliveres et al. 2016). Taxonomic diversity was also found to provide the strongest predictive power for rates of the energy flux of macroinvertebrate assemblages in tropical and temperate ecosystems (Barnes et al. 2016) and was the best predictor of stem biomass growth of trees (Grossman et al. 2017). The impact of taxonomic diversity on ecosystem processes is thereby expected to be nonlinear and to saturate so that change in ecosystem functioning accelerates when loss of taxonomic diversity increases (Cardinale et al. 2012). Changes in taxonomic diversity can therefore substantially alter the structure and functioning of whole ecosystems (Spehn et al. 2005, Cardinale et al. 2012) and the impact of a loss of taxonomic diversity on ecosystem processes can be similar to that of drought, ultraviolet radiation, climate warming, acidification, elevated CO_2, fire, and nutrient pollution (Hooper et al. 2012, Tilman et al. 2012).

However, there is growing consensus that taxonomic diversity measures alone are of limited suitability to comprehensively understand the underlying processes of diversity patterns (Weiher and Keddy 1995, McGill et al. 2006, Cadotte et al. 2013). One of the essential shortcomings of taxonomic diversity measures is, that they only mirror a small fraction of the overall diversity within an ecosystem (Lyashevska and Farnsworth 2012). In particular, taxonomic measures do not account for species identity and treat all species as evolutionarily independent and functionally equivalent (Petchey et al. 2004). Assembly processes, however, do not act on the number of species, but on their identity and distinctness. Likewise, the contribution of taxonomic diversity *per se* to the ecosystem processes is not well defined and taxonomic diversity measures can leave great parts of the variation in ecosystem functioning unexplained (Díaz and Cabido 2001, Cardinale et al. 2012). These shortcomings of taxonomic diversity measures led to a shift of the focus of biodiversity research from taxonomic approaches towards measures that account for ecological differences or similarities of species. So far, two major approaches have been developed: Phylogenetic measures that summarize the degree to which species differ in terms of their evolutionary history (Webb et al. 2002), and functional measures that summarize the degree to which species differ in terms of their functionally important traits (Petchey and Gaston 2002, Cadotte et al. 2013). Both types of measures are useful to gain deeper insights into *i)* the processes behind species assembly, *ii)* interactions between species and their environment, and *iii)* the functioning of ecosystem processes.

Phylogenetic diversity – a mirror for processes behind species assembly

Phylogenetic diversity (phylodiversity) is a measure of the phylogenetic relatedness among species. Assemblages that consist of distantly related species are phylogenetic more diverse (high phylodiversity) compared to assemblages that consist of closely related species (low phylodiversity). Phylodiversity, therefore, reflects the evolutionary history of assemblages and can reveal the processes which shaped assemblages (Webb et al. 2002, Cavender-Bares et al. 2009, Mouquet et al. 2012; but also see Gerhold et al. 2015). Indeed, phylodiversity was often used to study the processes behind the large-scale pattern of decreasing taxonomic diversity with increasing latitude or elevation (Kerkhoff et al. 2014). To explain these patterns, different ecological as well as historical processes were suggested (Wiens et al. 2006, Qian et al. 2015). Ecological processes comprise the trait- and niche based assortment of species along environmental gradients (environmental filtering), and competition between co-occurring species (Emerson and Gillespie 2008). Whereas historical processes include historical and biogeographic events such as changes in the location of landmasses, global climatic changes, and the formation of moun-

tains that influenced the speciation, extinction, and migration of species and therefore diversity patterns (Raven and Axelrod 1974, Ricklefs 2004, Hoorn et al. 2010). Only recently there is growing consensus that ecological, as well as historical processes, are jointly involved in forming patterns of biodiversity (Gaston 2000, Mittelbach and Schemske 2015).

A framework which joins both ecological and historical processes and allows to analyze assembly processes from a phylogenetic perspective is provided by the concept of phylogenetic niche conservatism (PNC; Wiens and Donoghue 2004). PNC is based on three main assumptions: *i)* Traits that influence the spatial distribution of species are phylogenetically conserved (Prinzing et al. 2008). *ii)* Thus, closely related species are ecologically more similar than distantly related species. *iii)* Species and clades retain their ancestral ecological niches (Wiens et al. 2010). In turn, PNC predicts that environmental filters influence closely related species in a similar manner (Wiens and Graham 2005). Environmental filtering should, therefore, lead to species assemblages that consist of species that are more closely related to each other than expected by chance (clustering; phylogenetic underdispersion). In contrast, competition is expected to limit the coexistence of closely related species due to similar niche requirements, leading to the mutual exclusion of closely related species. Thus, the PNC predicts that competition leads to assemblages that consist of species that are less closely related to each other than expected by chance (phylogenetic overdispersion; Webb et al. 2002, Cavender-Bares et al. 2009; but also see Cahill et al. 2008). These predictions of PNC can easily be tested along environmental gradients by comparing the observed phylogenetic assemblage structure with structures expected from null models (Kembel 2009). Moreover, comparisons of patterns from phylogenetic measures that emphasize different evolutionary timescales allow drawing conclusions about processes from the recent past to ancient evolutionary times.

In terms of biodiversity patterns, PNC is often considered in connection with the climatic history of the earth. Because tropical climates are the oldest currently existing climates (~ 146 mya; Raymo and Ruddiman 1992), the diversity of species within tropical lineages is especially high (time-for-speciation-effect; Wiens et al. 2010). The conservatism in traits and niches constrained tropical lineages to evolve adaptations to non-tropical conditions, and therefore the colonization of extra-tropical regions, that emerged only during the Eocene cooling (~ 50 mya; Wiens and Donoghue 2004, Graham 2011, Hawkins et al. 2014). PNC in combination with the time-for-speciation-effect therefore predicts decreasing species richness, phylodiversity, and mean clade age with decreasing tropicality, i.e. temperature (Gaston and Blackburn 1996, Wiens and Donoghue 2004, Wiens et al. 2006, 2010). So far, many studies found niche conservatism to be dominant in assemblages (Peterson 2011; but also see Losos 2008) and predictions of PNC are congruent with the pattern of decreasing taxonomic diversity with increasing latitudes (Hawkins et al. 2014, Qian et al. 2014). Nevertheless, studies of patterns along elevational gradients revealed contrasting results (Segovia et al. 2013, Qian 2014). Thus, it is still in doubt whether the PNC can be accepted as a general explanation for the trend of declining taxonomic diversity with decreasing temperature both at latitudinal and elevational gradients.

The PNC does not only provide the framework for studies of assembly processes but also bridges the gap to the functional diversity of assemblages and ecosystems (Maherali and Klironomos 2007). Still, under the assumption of phylogenetically conserved traits, phylodiversity should also represent the functional trait space of assemblages (Cavender-Bares et al. 2009, Letten and Cornwell 2015). Indeed, phylodiversity was found to better reflect the functional diversity of assemblages than taxonomic diversity measures and could even be correlated with ecosystem processes, such as biomass production and carbon sequestration (Cadotte et al. 2008, 2009b, Mouquet et al. 2012, Cadotte 2013). However, there is no direct link between phylodiversity and trait characteristics or ecosystem processes. Consequently, phylodiversity cannot be used as a universal predictor of ecosystem functioning (Graham et al. 2012, Venail et al. 2015). Nevertheless, the use of phylogenetic measures as a surrogate for functionality may be useful when the ecosystem process under consideration is complex and involves a large number of species and traits that are difficult to define or measure (Pakeman and Quested 2007, Srivastava et al. 2012). Instead of phylodiversity, traits are the more direct measure of the functioning of ecosystem processes. They are directly linked to interactions between species and their environment and define the functional space of assem-

blages (Petchey and Gaston 2006, Griffin et al. 2009, Song et al. 2014).

Functional diversity – traits form the basis for interactions between species and their environment

Traits capture essential aspects of the morphology, physiology, behavior, and phenology of species and provide the basis for interactions between species and their environment (Keddy 1992). Accordingly, the trait configuration defines the niche as well as the functional role of species within their abiotic and biotic environment, providing a mechanistic link between species identities, environmental conditions, and ecological processes (Blackburn and Gaston 2001, McGill et al. 2006, Swenson and Weiser 2010). The link between species traits and ecosystems is reciprocal. On the one hand, traits determine the ecological response of an organism to environmental conditions and therefore affect the distribution of species and the composition of species assemblages. On the other hand, traits also determine the effects of organisms on ecosystem properties and the provision of ecosystem processes (Díaz et al. 2007, de Bello et al. 2010, Cadotte et al. 2011).

Body size is often considered as the most important morphological trait of organisms because it strongly affects their overall fitness and the position and interactions within food webs (LaBarbera 1989, Akin and Winemiller 2008). For animals, body size determines fecundity, resource requirements, thermoregulatory abilities, and competitiveness (Whitman 2008) and thus, plays an important role in the distribution of species (Nock et al. 2016, Schellenberger Costa et al. 2017). According to Bergmann's rule, the intra- and interspecific body size of closely related endothermic animals increases with decreasing temperature, e.g. along latitudinal gradients (Bergmann 1847). For arthropods and other ectotherms, several examples for positive as well as negative body size clines with decreasing temperature exist, both at latitudinal and elevational gradients. The generality of intra- and interspecific body size clines of ectotherms is therefore still intensively debated (Angilletta et al. 2004, Chown and Gaston 2010, Shelomi 2012). Moreover, other morphological traits will additionally influence the fitness of organisms and consequently the distribution of species, making relationships between species distributions, body size clines, and environmental factors more complex (Land 1997, Picaud and Petit 2008). Yet, besides body size, other morphological traits are highly underrepresented in studies of size clines along environmental gradients.

Functional diversity – a driver of ecosystem processes

Body size also influences interactions with other organisms, can indicate the trophic position within food webs and determines the functional role of species in their environment (Akin and Winemiller 2008). Here again, other functional traits additionally affect these aspects. Functional traits are therefore expected to be strongly linked with the functioning of ecosystem processes, e.g. herbivory, predation, nutrient cycling, and biomass production (Petchey and Gaston 2006, Gagic et al. 2015). These processes provide the basis for stability within ecosystems and for the provisioning of ecosystem services. The functional differentiation of traits can be measured as functional trait space and is usually referred to as functional diversity (Laliberté and Legendre 2010, Lamanna et al. 2014). The functional diversity of assemblages and ecosystem processes are generally positively related. The theory assumes that variations in the resource use of species (for example via herbivory or predation) are represented by the functional trait diversity of associated species. A greater complementarity in resource use should lead to more complete and/or efficient use of resources and therefore increases the respective ecosystem process (Díaz and Cabido 2001, Petchey and Gaston 2006). Moreover, the diversity and redundancy of functional traits enhance the resilience of ecosystem processes in the face of degradation and environmental changes (Biggs et al. 2012).

Due to the tight links between taxonomic and functional diversity with ecosystem processes, anthropogenic changes that affect the biodiversity within ecosystems can also affect ecosystem functioning (Cardinale et al. 2012, Isbell et al. 2013, Haddad et al. 2015). However, a loss of species does not necessarily lead to changes in the functioning of ecosystem process (Schwartz et al. 2000). Instead, the impact is highly species-specific as it depends on the traits and functionality of the respective species and can be additionally affected by abiotic and/or biotic conditions (Mazel et al. 2014, Gagic et al. 2015, Wohlgemuth et al. 2017). The ongoing tremens-

dous anthropogenic impacts on biodiversity therefore urgently require a continuous monitoring of the status and functioning of ecosystems (Palmer and Febria 2012). For the monitoring of habitat quality and integrity, taxonomic indicators have already proven to be useful (Siddig et al. 2016; but also see Gossner et al. 2014). The taxonomic diversity of plants and ants for example effectively indicate the richness and abundance of butterflies and birds in grasslands (Peters et al. 2016) and the composition of ant and orthopteran assemblages are suitable indicators for the succession in riparian or steppe grassland habitats (Gollan et al. 2011, Fartmann et al. 2012). For the monitoring of ecosystem functioning, however, trait-based functional measures are more promising because they are more directly linked with ecosystem processes than taxonomic measures. Measures of functional diversity could therefore meaningfully expand the existent taxonomic indicators for ecosystem monitoring (Díaz et al. 2007, Vandewalle et al. 2010).

Process-indicators with especially high prospects of success are such that base on functional traits of taxa which play important roles in the functioning of ecosystem processes (Noss 1999, Palmer and Febria 2012). Important relationships exist for example between the size, diameter, and wood density of terrestrial vascular tree species and biomass production, and between the body size, mobility, and starvation capacity of predatory insects and the predation on herbivores in terrestrial ecosystems (de Bello et al. 2010; also for a comprehensive review of 247 studies on linkages between functional traits and ecosystem processes). Despite relationships between functional traits and ecosystem processes, the suitability of trait-based measures as indicators for a monitoring of ecosystem processes under changing environmental conditions has rarely been tested (Pinto et al. 2014, Walters and Scholes 2017).

Aims of the thesis

Understanding the patterns and processes of the taxonomic, phylogenetic, and functional components of biodiversity and their relationships with the functioning of ecosystem processes is a fundamental basis for effective conservation management. My thesis therefore focuses on three different questions related to changes in the taxonomic, phylogenetic and functional diversity of species assemblages along environmental gradients. In particular, I conducted three studies along tropical elevation gradients to investigate *i)* assembly processes, *ii)* size clines of morphological traits along a temperature and productivity gradient, and *iii)* relationships between abiotic and biotic factors, taxonomic and functional aspects of keystone taxa, and their effects on an important ecosystem process. To match the respective research question, each study focuses on an independent study taxon and study area.

i) In the first study (chapter 2), I was interested in the interplay of historical evolutionary and recent ecological processes that shape today's tree species assemblages in the Andes of South Ecuador – a hotspot of terrestrial biodiversity. To do so, I tested predictions of PNC for species richness, phylodiversity, and family age along an elevational gradient. A phylogenetic tree, constructed for the tree species of my study area, combined with age estimates of the phylogenetic nodes, provides the basis for the first study. I used linear regression models to analyze relationships between elevation (as a proxy for temperature) and three different metrics of the phylogenetic composition of tree assemblages. By doing so, I aimed to disentangle assembly processes acting at time scales from the recent past to the ancient evolutionary history.

ii) In the second study (chapter 3), I focused on the morphological traits of species assemblages. Here, I studied patterns of interspecific changes of morphological traits of orthopteran assemblages in response to changing environmental conditions along an elevational gradient at Mt. Kilimanjaro, Tanzania. Specifically, I investigated relationships between both temperature and productivity and the body size, wing length, hind femur length, and eye size of orthopteran assemblages using Bayesian linear mixed models.

iii) In the third study (chapter 4), I aimed to test the suitability of ants as a biological indicator of responses to environmental changes and of an important ecosystem process. To do so, I compared the suitability of taxonomic and functional measures of ant assemblages as a functional indicator for the ecosystem process predation of herbivorous arthropods in the mountain rainforest ecosystem in Southern Ecuador. In particular, I used a path model approach which allowed me to disentangle the relationships between temperature, season, habitat degradation and the incidence, taxonomic rich-

ness, and functional richness of ants, and their consequences for predation of herbivorous arthropods.

The three studies have either been published or have been submitted to scientific journals. The background knowledge for the three studies is given in the respective chapters, which can, therefore, be read independently.

Study areas

I did the three field studies along extensive elevational gradients in two different tropical regions: The eastern Cordillera of the Andes in South Ecuador, and the slopes of Mt Kilimanjaro, Tanzania.

I worked in South Ecuador on the eastern Cordillera of the Andes to test predictions of the phylogenetic niche conservatism hypothesis on tree assemblages (chapter 2) and to test the suitability of ants as an indicator for ecosystem changes and predation (chapter 4). The Andes are particularly suited for studies that seek to understand historical and recent processes behind the patterns of species assemblages because the highest elevation habitats are relatively young. The Andean uplift began in the Paleogene around 65 mya and ended only between 2 mya and 15,000 years ago (Hoorn et al. 2010). Therefore, processes from both the biogeographic history of lineages as well as from more recent ecological processes should be reflected in the recent species assemblages along Andean slopes. The studied elevational gradient in South Ecuador is part of the tropical Andes biodiversity hotspot (Myers et al. 2000) and comprises lands in the provinces of Loja and Zamora-Chinchipe within and around the Podocarpus National Park and the Reserva Biológica San Francisco. The study area spans elevations from ~ 1,000 to ~ 3,000 m a.s.l. and includes protected areas consisting of natural primary forest, as well as patches of degraded secondary forests in a matrix of active or inert pastures for cattle grazing outside of the protected areas (Curatola Fernández et al. 2015). The climate is perhumid and annual rainfall is high throughout the year and increases with elevation, whereas the mean annual air temperature decreases with increasing elevation following the typical moist adiabatic lapse rate of ~ -0.6 K (100 m)$^{-1}$ from 20 °C at 1,000 m a.s.l., to 9.5 °C at 3,000 m a.s.l. (Bendix et al. 2008a, 2008b, Rollenbeck and Bendix 2011).

The slopes of Mt. Kilimanjaro in Tanzania were used to study the relationships between changes in elevation and productivity with ecologically important morphological traits of Orthopteran assemblages (chapter 3). Mt. Kilimanjaro offers different ecosystems with highly heterogeneous characteristics along its slopes that are particularly suitable for studies of morphological changes of species assemblages with changing environmental conditions (Hemp 2006). The environmental gradient comprises elevations from ~ 700 to ~ 4,400 m a.s.l. The area is characterized by savanna grass- and woodlands that are mainly converted into agricultural lands at the lower elevations (~ 700 to ~ 1,000 m a.s.l.), multi-cropping agroforestry systems at mid-elevations (1,000 m a.s.l. to 1,800 m a.s.l.), montane to sub-alpine forests at high elevations (1,800 m a.s.l. and 3,700 m a.s.l.), and a landscape almost bare of vegetation above 4,500 m a.s.l. The precipitation peaks between March and May and between October and November and the mean annual land surface temperature decreases with increasing elevation from 20 °C at ~ 1,500 m a.s.l. to 8.5°C at ~ 4,5000 m a.s.l. (Maeda and Hurskainen 2014).

Chapter 2

Phylogenetic niche conservatism does not explain elevational patterns of species richness, phylodiversity and family age of tree assemblages in Andean rainforest

with
Jürgen Homeier | Nixon Cumbicus | Jaime Peña | Jörg Albrecht |
Birgit Ziegenhagen | Jörg Bendix | Roland Brandl | Nina Farwig |

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Summary

Phylogenetic niche conservatism (PNC) is the tendency of species within a clade to retain ancestral traits and to persist in their primary ecological niches on geological time scales. It links evolutionary and ecological processes and has been hypothesized to explain patterns of species richness and the composition of species assemblages. Decreasing patterns of species richness along latitudinal gradients were often explained by the combination of ancient tropical climates, trait retention of tropical lineages and environmental filtering. PNC also predicts decreasing phylodiversity and family age with decreasing tropicality and has been invoked to explain these patterns along climatic gradients across latitudinal as well as elevational gradients. However, recent studies on tree assemblages along latitudinal and elevational gradients in South America found patterns contradicting the PNC framework. Our study aims to shed light on these contradictions using three different metrics of the phylogenetic composition that form a gradient from recent evolutionary history to deep phylogenetic relationships. We analyzed the relationships between elevation and taxonomic species richness, phylodiversity and family age of tree assemblages in Andean rainforests in Ecuador. In contrast to predictions of the PNC we found no associations of elevation with species richness of trees and increasing clade level phylodiversity and family age of the tree assemblages with elevation. Interestingly, we found that patterns of phylodiversity across the studied elevation gradient depended especially on the deep nodes in the phylogeny. We therefore suggest that the dispersal of evolutionarily old plant lineages with extratropical origins influences the recent composition of tree assemblages in the Andes. Further studies spanning broader ecological gradients and using better resolved phylogenies to estimate family and species ages are needed to obtain a deeper mechanistic understanding of the processes that drive the assembly of tree communities along elevational gradients.

Introduction

Although various exceptions at low taxonomic levels exist (Algar et al. 2009, Romdal et al. 2013), the decrease of species richness with increasing latitude is one of the most consistent patterns in ecology and biogeography (Lawton 1999, Gaston 2000, 2007, Hillebrand 2004). Numerous hypotheses have been proposed to explain this large scale pattern invoking ecological, historical, and evolutionary processes (e.g. Willig et al. 2003, Wiens et al. 2006). On the one hand, variables related to current climate and productivity were used to explain these gradients of species richness from an ecological point of view (for a recent meta-analysis see Field et al. 2009). For instance, optimum plant growth is found under humid conditions at tropical latitudes, whereas colder seasonal and, therefore, harsher climates decrease the probability that abiotic conditions match the tolerances of species. Therefore the match of niche requirements with the abiotic conditions, leads to the assortment of species along environmental gradients (environmental filtering), which influences not only species richness (Graham and Fine 2008, Pavoine and Bonsall 2011) but also the composition of regional species pools and local assemblages (Lebrija-Trejos et al. 2010, Pavoine and Bonsall 2011, Spasojevic and Suding 2012). On the other hand, the species pools on which these ecological processes operate are shaped by biogeographical and historical events that occurred during the geological history of the Earth (Raven and Axelrod 1974, Ricklefs 2004). For example, the breakup of the super-continent Gondwana (Morley 2003) influenced the location of landmasses, the global climate and the formation of mountains. This had consequences for speciation, extinction and dispersal, which in turn influenced the continental as well as regional species pools and thereby also local assemblages (Briggs 1995, Hoorn et al. 2010). Therefore, historical (e.g. speciation, extinction and migration) and ecological (e.g. environmental filtering) processes are not in conflict (Wiens and Donoghue 2004, Johnson and Stinchcombe 2007; but also see Algar et al. 2009), but should be considered jointly for a comprehensive understanding of recent patterns in species richness (Mittelbach and Schemske 2015).

The concept of phylogenetic niche conservatism (PNC) bridges the gap between historic and ecological processes (Ricklefs and Latham 1992, Wiens and Donoghue 2004). Niche conservatism in general describes the tendency of species and entire clades to retain their ancestral ecological traits (Wiens et al. 2010). If traits that influence the spatial distributions of species are phylogenetically conserved (which was found multiple times for plants; Chazdon et al. 2003; Prinzing et

al. 2008), closely related species should have more similar traits than distantly related species and consequently the distribution of these species should be determined by similar environmental filters (Wiens and Graham 2005). Furthermore, PNC is closely linked with the time-for-speciation-effect (TSE) as the low probability of species to colonize habitats with different environmental conditions will lead to an accumulation of species in areas, in which a clade evolved (see review in Stephens and Wiens 2003). The combination of PNC and TSE was often used to explain the pattern of decreasing species richness along the latitudinal gradient from the tropics to the Arctic and Antarctic (Wiens et al. 2010). In this context, the PNC-TSE framework refers to the age of tropical (warm and wet) climates: Tropical climates are the oldest currently existing climates as the Earth's surface has been mainly tropical since the early Cretaceous (~ 146 mya; Raymo and Ruddiman 1992), whereas temperate and arctic environments have existed only since the global cooling during the Eocene (~ 50 mya; Graham 2011). According to the TSE, tropical lineages, therefore, had a considerable time span and area in which to speciate, leading to high species numbers within tropical lineages (Stephens and Wiens 2003, Wiens and Donoghue 2004). In turn, PNC implies that species in tropical lineages are adapted to tropical climates and the conservatism in traits constrains the evolution of adaptations to non-tropical conditions (e.g. cold-tolerance) and the colonization of extra-tropical regions (Wiens and Donoghue 2004, Wiens et al. 2006, 2010). Overall, PNC predicts that adaptation to tropical climate, niche conservatism and environmental filtering lead to a decrease of species richness, phylodiversity and age of clades with decreasing tropicality.

To date, patterns predicted by the PNC have been analyzed with emphasis on latitudinal gradients and many analyses detected results consistent with the PNC (Hillebrand 2004, Hawkins et al. 2011, 2014, Giehl and Jarenkow 2012, Romdal et al. 2013, Jansson et al. 2013, Qian et al. 2013, 2014, Kerkhoff et al. 2014; but see Huang et al. 2014, Boucher-Lalonde et al. 2015). As PNC should apply to different sorts of environmental gradients and elevational gradients are known for their possible contribution to answer important questions of macroecology (Körner 2000; for a review of elevational gradients see Rahbek 1995, 2005), PNC was also used to explain patterns of species richness along elevational gradients (Kozak and Wiens 2010). In Indonesia, for example, phylodiversity decreased with increasing elevation (Dossa et al. 2013) – a result consistent with PNC. However, patterns contradicting PNC were found in two studies which reported older instead of younger tree assemblages at high elevations and high latitudes. This was explained by the dispersal of ancient Gondwanan elements (Segovia et al. 2013, Qian 2014).

We selected a site in the Tropical Andes' hotspot of biodiversity (Myers et al. 2000), characterized by montane rain forests in Ecuador, for a further test of PNC along an elevational gradient. The tropical Andes are of great value for studying relationships between temperature and species assembly in plant assemblages (Antonelli et al. 2009, Pennington et al. 2010), especially in the context of PNC. First, the Andean mountain chain is geologically relatively young – its orogeny began in the Paleogene around 65 mya (which overlaps temporally with the emergence of temperate climate zones), but the Andes reached their highest and final elevations only between 2 mya and 15.000 years ago (Hoorn et al. 2010). Second, the Andean uplift had important effects on ecosystems through the creation of high elevation habitats and by acting as a barrier for the dispersal of tropical and corridor for dispersal of cold adapted species (Hoorn et al. 2010, Luebert and Weigend 2014). Consequently, the effect of (historical) biogeographic and of recent ecological processes should have left an imprint on the composition of the species assemblages along Andean slopes. We tested whether the predictions of PNC hold true for species richness, phylodiversity and family age along an elevational gradient in the Andes of Ecuador. In contrast to most of the published studies, we use three different metrics characterizing the phylogenetic composition of tree assemblages that cover a gradient from recent evolutionary history to deep phylogenetic relationships.

Methods

Study area

The study area is located in South Ecuador at 1000 – 3000 m a.s.l. on the eastern Cordillera of the Andes in the provinces of Loja and Zamora-Chinchipe. The topography in the study area is generally very steep (20–50°). Soil conditions are heterogeneous with a better nutrient supply at

lower elevations and in valleys compared to more unfavorable nutrient conditions for plant growth at high elevations (Wilcke et al. 2008, Wolf et al. 2011, Werner and Homeier 2015). The climate of the study area is perhumid with peak rainfall occurring in June, July and August (Rollenbeck and Bendix 2011). Annual rainfall is high with ~ 2000 mm at 1000 m (Zamora), ~ 2200 mm at 2000 m (ECSF-Met. Station; ~ 2300 mm including occult precipitation) and ~ 4800 mm at 3000 m a.s.l. (Cerro Met. Station; ~ 6700 mm including occult precipitation; Bendix et al. 2008a, 2008b). However, it should be stressed that the local amount of annual rainfall is strongly influenced by the strength of topographic sheltering against the easterlies (Bendix et al. 2006, Rollenbeck and Bendix 2011, Wagemann et al. 2015). The mean annual air temperature decreases with elevation from 20.0 at 1000 m to 15.5 at 2000 m to 9.5 °C at 3000 m a.s.l., with a typical moist adiabatic lapse rate of around -0.6 K $(100\ m)^{-1}$ (Bendix et al. 2008b).

Study design

The study design comprised three different elevation levels (~ 1000 m a.s.l.; ~ 2000 m a.s.l. and ~ 3000 m a.s.l.) which harbor three different forest types (evergreen premontane rain forest at 1000 m, evergreen lower montane rain forest at 2000 m and evergreen upper montane rain forest at 3000 m a.s.l.; see Homeier et al. 2008 for more details). Each elevation level contained 18 permanent plots, each 20 m x 20 m in size. The minimum distance between all plots was 0.02 km and the maximum distance was 24 km, with a mean of 14 km (maximum distance between plots within the same elevation level was 1.5 km, mean plot distance within the elevation levels ranged from 292 m to 704 m). For more detailed information on the location of the study sites see Supplementary Table 2.1 in Appendix, for a map of the study area with study site locations see Jantz et al. 2014. All plots were located in homogenous mature forest without visible natural or human disturbance. In each plot all trees with a dbh ≥ 5 cm (at 1.3 m height) were recorded and determined to species level where possible (69 %), otherwise to morpho-species at genus level (31 %). Families were classified after APG III (The Angiosperm Phylogeny Group 2016). Tree ferns (Cyatheales) were excluded from the present analysis.

Phylogenies

We used the latest available and best resolved phylogenetic megatree (R20120829mod.new; Gastauer et al. 2016; Supplementary Methods 2.1 in Appendix) to construct the phylogeny for our analysis of phylodiversity. We used the online-tool Phylomatic (http://www.phylodiversity.net/phylomatic; Webb et al. 2002) where we inserted the megatree and the list of observed tree taxa. Phylocom then assigned the 420 tree species on our plots to the megatree resulting in a phylogeny without branch lengths. To assign the branch length of the phylogenetic tree we used the 'bladj' module of Phylocom. We accessed the age file provided by Gastauer et al. (2016) which is based on age estimates by Bell et al. (2010; Supplementary Table 2.2 in Appendix). The 'bladj' algorithm uses the provided age estimates for specific nodes in the phylogeny and distributes the remaining undated nodes evenly between the estimated nodes (Webb et al. 2008). This two-step approach is widely used in ecological studies using plant phylogenies (Swenson et al. 2007, Webb et al. 2008, Kress et al. 2009, Slik et al. 2009; but also see Swenson et al. 2006).

Diversity components

Taxonomic richness

As the number of species depends on sample size (Colwell et al. 2012) we applied a rarefaction method (Hurlbert 1971) using the function 'rarefy' in the package 'vegan' for R (Oksanen et al. 2016) to calculate the expected species richness in random subsamples of 17 individuals (smallest number of individuals sampled within a plot) per plot.

Phylogenetic diversity

We used two different measures for phylogenetic diversity, the mean nearest taxon distance (MNTD) which resembles the mean distance separating each individual in the assemblage (plot) from its closest relative and the mean pairwise distance (MPD) between individuals of all species in each assemblage. The MNTD is a useful measure to detect patterns close to the tips of the phylogenetic tree. In contrast, MPD uses pairwise phylogenetic distances between individuals and is useful to detect tree-wide patterns of phylogenetic clustering and evenness for locally co-occuring species (Kembel et al 2010). We used a null model approach as proposed by Swenson et

al. (2012) to test for phylogenetic clustering and overdispersion in the local tree assemblages. Following the approach we shuffled the tip labels of the phylogeny of our local tree 1000 times and calculated standardized effect sizes for both phylodiversity metrics (sesMNTD and sesMPD) as ses$X$ = ($X_{observed}$ − mean(X_{random})) / sd(X_{random}), where $X_{observed}$ was the observed value of either MNTD or MPD, mean (X_{random}) was the mean of the randomizations of the null-model and sd (X_{random}) was the standard deviation of the randomly calculated values of each metric. The calculations of both phylodiversity metrics were conducted using the packages 'ape', 'picante' and 'phytools' for R (Paradis et al. 2004, Kembel et al. 2010, Revell 2012).To test the effect of the gymnosperm species in our dataset we additionally calculated standardized effect sizes of both phylodiversity metrics for the dataset without gymnosperms (excluded species: *Podocarpus oleifolius*. and *Prumnopitys montana*, both Podocarpaceae).

Age of families

We used Davies et al. (2004) family ages (Supplementary Table 2.3 in Appendix) instead of ages by Bell et al. (2010) to calculate mean family ages on our plots because family ages by Davies et al. (2004) match fossil records closer than the ones by Bell et al. (2010; see method section in Hawkins et al. 2014). As phylogeny of Davies et

Table 1. List of the ten oldest and five youngest tree families (those with phylogenetic ages > 100 myr and < 40 myr) recorded on our study plots. The table reports family, family age, total species richness, abundance (sum of individuals recorded on the three elevation levels), historical origin (reference: Raven and Axelrod 1974). Note that the most abundant species per elevation level comprised 100 at 1000 m, 69 at 2000 m and 133 individuals at 3000 m a.s.l. and the most abundant family comprised in total 528 individuals (Melastomataceae).

			Abundance at			
Family	Age [myr]	Species richness	1000 m a.s.l.	2000 m a.s.l.	3000 m a.s.l.	Biogeographic origin
Chloranthaceae	143.8	7	5	40	40	Laurasia
Podocarpaceae (gymnosperms)	132.7	2	0	10	33	South Gondwana
Sabiaceae	127.2	5	4	2	3	West Gondwanaland, Australasia
Proteaceae	126.1	5	7	4	1	West Gondwanaland, Australasia
Hernandiaceae	116.7	1	0	2	0	West Gondwanaland, Australasia
Siparunaceae	109.5	2	0	7	5	Unassigned
Winteraceae	106.8	1	0	0	17	West Gondwanaland
Picramniaceae	103.9	2	3	0	0	unassigned
Myricaceae	101.5	1	0	0	11	Laurasia
Palmae	101.0	4	3	4	2	unassigned
Lamiaceae	39.7	1	0	2	0	Laurasia
Primulaceae	36.7	6	0	30	79	West-Gondwanaland-Laurasia
Caryophyllales b	30.6	4	19	0	0	Laurasia
Urticaceae	25.2	5	22	18	0	Laurasia
Moraceae	25.2	21	200	35	0	Laurasia

al. (2004) comprised only angiosperm species we added the age for the gymnosperm family Podocarpaceae manually (132.7 my; Lu et al. 2014). We calculated the mean family age by allocating each species the age of its family and averaged the age across the species (unweighted mean family age) and across individuals (abundance weighted mean family age) at each plot. We calculated the mean family ages also after excluding gymnosperms.

Using mean values across species and correlating these with other variables extracted from the matrix of species occurrences (e.g. species richness) may lead to spurious correlations (Zelený and Schaffers 2012). This bias may also lead to spurious correlations with independent variables not extracted from the species by site matrix as long as these variables covary with species richness. To correct for this bias we calculated the standardized effect sizes of the mean family ages (ses family age) using the same approach as for the phylodiversity by randomizing the assigned family ages of the species 1000 times (see also Zelený and Schaffers 2012).

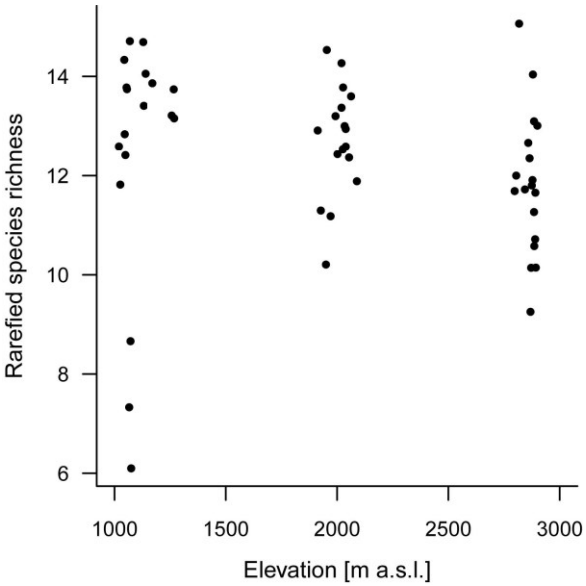

Figure 1. Rarefied species richness (n = 17 trees) per study plot in relation to elevation

Statistical analyses

We tested for relationships between elevation and *i)* rarefied species richness, *ii)* sesMNTD, *iii)* sesMPD, and iv) mean family age of species

Table 2. Table of statistical models for species richness and various metrics of the phylogenetic composition of tree assemblages in Southern Ecuador. We show results of linear models for relationships between rarefied species richness, standardized effect sizes of phylodiversity measure at the tip (sesMNTD) and at the clade level (sesMPD) and observed and standardized (ses) mean family ages. For all metrics (except rarefied species richness) we model two variants: one including gymnosperms and one excluding gymnosperms (column G). For each model we report intercept (Inter.), multiple R^2 (R^2), and degrees of freedom (df), as well as the slopes, t-value (slope divided by standard error) and error probability (P). For the standardized effect sizes we additionally specified the number of values < 0 and < - 2.

		Elevation				Species richness						
	G	Inter.	Slope	t-value	P	Slope	t-value	P	R^2	df	< 0	< - 2
Rarefied species richness	Yes	13	-3.2×10^{-4}	-0.94	0.35				0.017	52		
sesMNTD	Yes	- 0.16	1.7×10^{-4}	1.0	0.30	-0.065	-1.0	0.32	0.045	51	39	2
sesMNTD	No	0.63	1.7×10^{-4}	1.0	0.31	-0.092	-1.4	0.16	0.05	51	41	3
sesMPD	Yes	-1.9	7.2×10^{-4}	4.5	< **0.001**	0.035	0.54	0.59	0.28	51	35	0
sesMPD	No	-0.39	-1.7×10^{-4}	-0.85	0.40	-0.014	-0.18	0.86	0.01	51	46	9
Raw mean family age	Yes	38	4.9×10^{-3}	4.4	< **0.001**	1.7	3.7	< **0.001**	0.36	51		
Raw mean family age	No	39	4.1×10^{-3}	3.7	< **0.001**	1.6	3.6	< **0.001**	0.31	51		
ses mean family age	Yes	-2.9	6.6×10^{-4}	3.6	< **0.001**	0.072	0.97	0.34	0.21	51	39	7
ses mean family age	No	-2.7	5.5×10^{-4}	3.0	**0.0047**	0.073	0.96	0.34	0.15	51	41	8

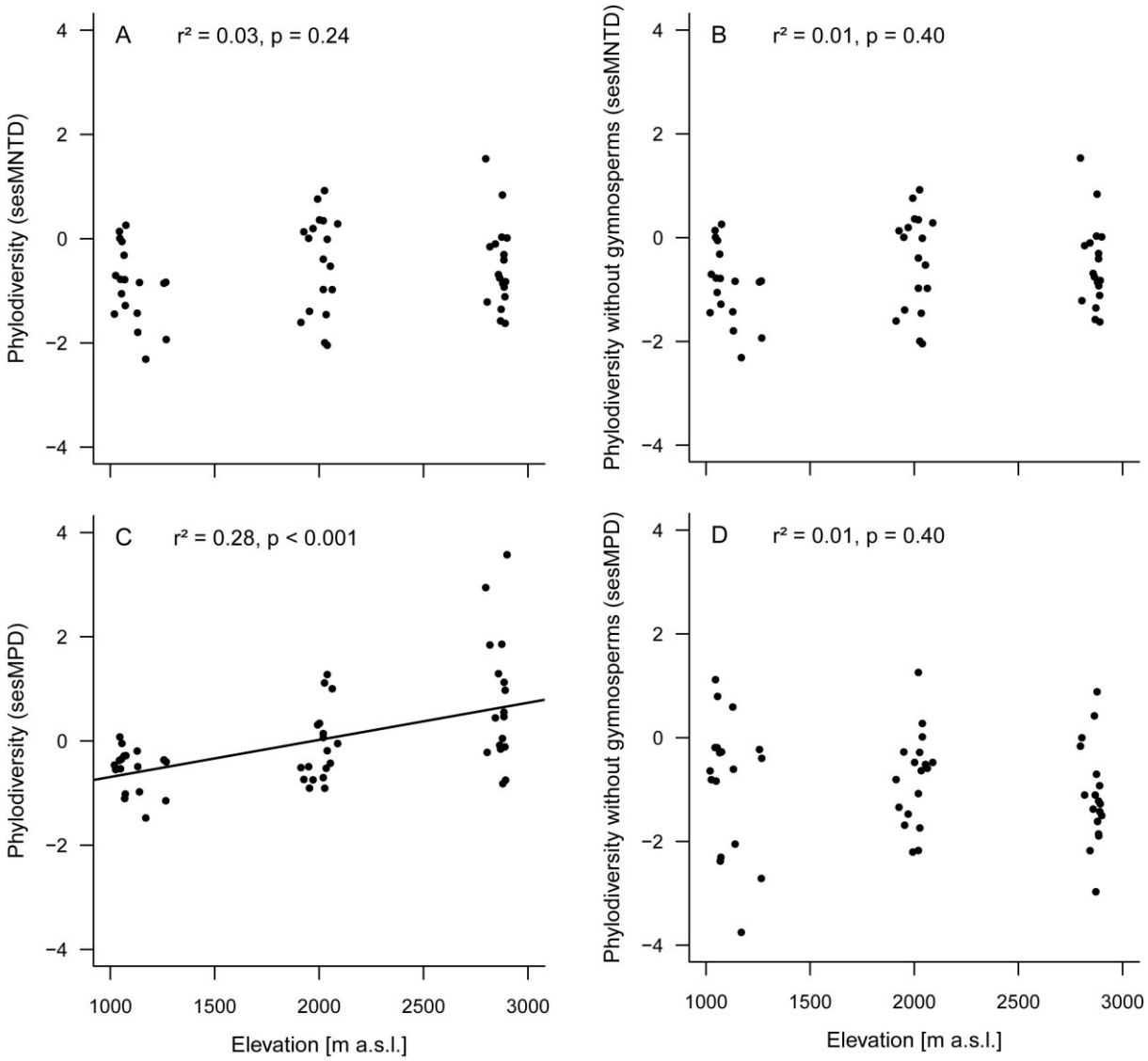

Figure 2. Observed relationships between the different measures of phylodiversity of the tree assemblages (A, C) and of assemblages after removing gymnosperms (B, D) and elevation. For the tip level phylodiversity (sesMNTD; standardized effect size of the mean nearest taxon distance) we observed neither a significant relationship between sesMNTD for the complete tree assemblage (A) nor after excluding gymnosperms from the dataset (B). We observed a significant positive relationship between sesMPD for the complete tree assemblage (C) and no significant relationship after excluding gymnosperms from the dataset (D). Line indicates significant linear relationship ($p < 0.05$).

within the tree assemblages in our study plots using linear models. To account for the effect of species richness on our measures of phylogenetic diversity, we included rarefied species richness as a covariate in models *ii)*, *iii)* and *iv)*. We compared the patterns of phylodiversity and phylogenetic family age for the complete assemblages and for the assemblage without gymnosperms. Additionally we tested for a correlation between observed and standardized MNTD and MPD values and mean family ages for the complete and the reduced dataset, respectively. All statistical analyses were done in the 'R' environment (R Core Team 2014).

Results

Species richness

Within our 54 study plots we recorded in total 3740 tree individuals (dbh ≥ 5 cm), belonging to 420 species, 178 genera and 72 families. Two species were gymnosperms (*Podocarpus oleifolius* and *Prumnopitys montana*). The most species rich families were Lauraceae (47 species), Rubiaceae (39 species), and Melastomataceae (37 species). The original numbers of individuals and species differed between the elevation levels: We found 994 tree individuals representing 177 spe-

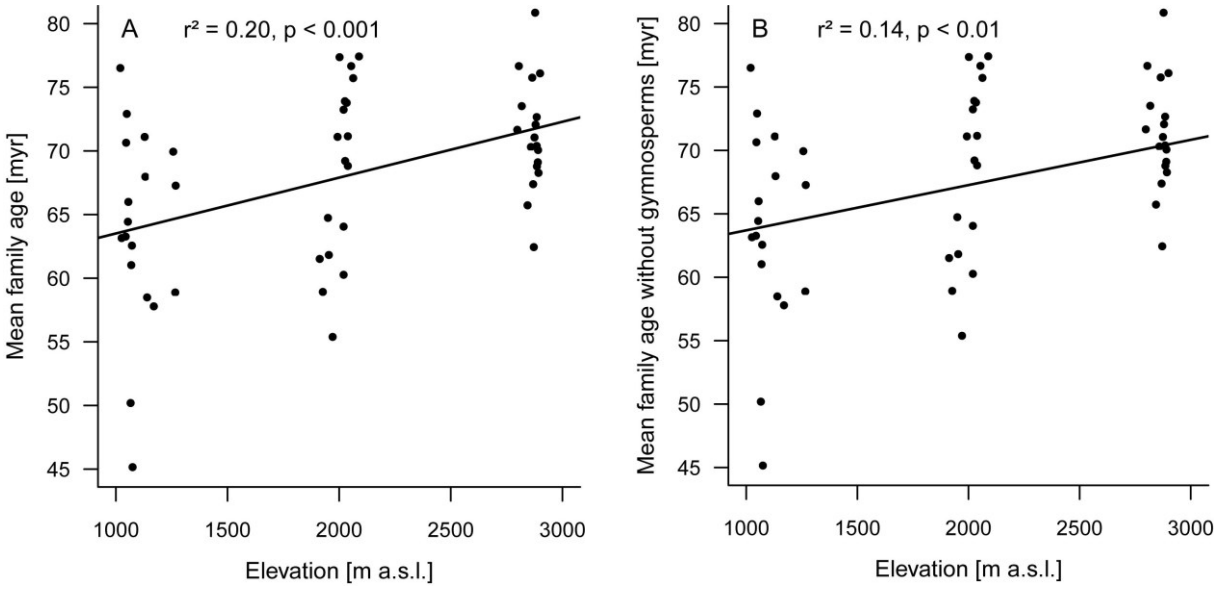

Figure 3. Relationship between mean family age of species weighted by abundance and elevation. We observed a significant positive relationship between mean family ages and elevation for the complete tree assemblage (A) and after excluding gymnosperms from the calculation of the mean family age (B). Lines indicate significant linear relationships ($p < 0.05$).

cies at 1000 m, 1172 individuals and 187 species at 2000 m, and 1574 individuals and 99 species at 3000 m a.s.l. The two gymnosperm species only occurred on the mid- and high elevation plots, the three youngest species only on the low- and mid elevation plots (Table 1). The rarefied species richness for a random sample of 17 tree individuals on each of the 400 m^2 plots ranged from 6.1 to 15 (12 ± 1.8; mean ± sd). There was no significant relationship between rarefied species richness and elevation (Fig. 1; Table 2).

Phylodiversity

For sesMNTD and sesMPD, effect sizes were mostly negative (63 – 82 % of values < 0; Table 2) indicating that the composition of assemblages was generally clustered. However, only few effect sizes were significantly clustered (standardized effect size < -2; Table 2). There was no significant relationship between elevation and phylodiversity with emphasis on the tip level (sesMNTD; Fig. 2 A; Table 2). The phylodiversity with emphasis on the clade level (sesMPD) increased with elevation with no additional effect of rarefied species richness (Fig. 2 C; Table 2). Excluding gymnosperms from the dataset we found neither an association of elevation with sesMNTD nor with sesMPD (Fig. 2 D; Table 2).

Age of species

The family age in the study plots ranged from 25.2 myr (species from the family Moraceae and Urticaceae) to 143.8 myr (species from the family Chloranthaceae). The two gymnosperm species Prumnopitys montana and Podocarpus oleifolius both from the family Podocarpaceae belonged to the second oldest family in our tree assemblage with an age of 132.7 myr. We found a significant increase of the mean family age of species with elevation with an additional significant association with the rarefied species richness (Fig. 3 A; Table 2). The pattern was also significant for the standardized effect size of mean family age (Supplementary Figure 2.1 A in Appendix). Species richness was not related to the standardized effect size of mean family age suggesting that the significant contribution of species richness in the model of the raw mean family ages is due to a bias introduced by compositional similarity (see Material and Methods).

The relationship between observed and standardized mean family age and elevation and the additional association with species richness was still significant when gymnosperms were excluded from the dataset (observed age: Fig. 3 B; Table 2; standardized age: Supplementary Figure 2.1 B in Appendix; Table 2). The observed and standardized MNTD values were not significantly correlated with mean family age for the

complete and reduced dataset excluding gymnosperms (all $r^2 < 0.034$, all $p > 0.18$, df = 52). The observed and standardized MPD values were positively correlated with mean family age for the complete dataset (MPD: $r^2 = 0.45$; sesMPD: $r^2 = 0.29$, both $p < 0.001$, df = 52); and also for the data set excluding gymnosperms (MPD: $r^2 = 0.46$; sesMPD : $r^2 = 0.31$, both $p < 0.001$, df = 52).

Discussion

Overall the tree assemblages in our study plots were phylogenetically clustered suggesting that environmental filtering mainly drives community assembly. Furthermore, elevation was not related to species richness of trees across the sampled plots, whereas clade level phylodiversity and family age of tree assemblages increased with elevation. Therefore, our results do not support the phylogenetic niche conservatism hypothesis (PNC). Considering only angiosperms, we found no relationship between elevation and phylodiversity but a positive relationship between elevation and family age of tree species. This suggests that evolutionary patterns of Andean tree assemblages seem to be more distinct from predictions of the PNC when the phylogenetic structure deep within the phylogeny of plants is taken into account.

Taxonomic richness

Contrary to our expectation, species richness corrected for sample size did not decrease with increasing elevation. This finding contrasts the general hump-shaped or decreasing pattern of species richness along elevational gradients (Rahbek 1995, Lomolino 2001). Three possible reasons might explain our findings: First, the high number of tree species at the mid and high elevation level on our plots and the high percentages of endemism for the Ecuadorian vascular plant flora above 1500 m a.s.l. (as many as 200 species are endemic in the Podocarpus National Park; Jorgensen and León-Yánez 1999, Valencia et al. 2000, Kessler 2002) could indicate high speciation rates in lineages adapted to high elevations (Homeier et al. 2010). Second, our study design did not cover the entire elevation range of all tree species and our plots were not distributed continuously along the gradient (Rahbek 1995). Third, factors other than elevation may have influenced the distribution of species richness. One likely driver is e.g. the high habitat heterogeneity along the studied gradient caused by a combination of complex topography and related climate and soil conditions (Homeier et al. 2010, Peters et al. 2014b, Werner and Homeier 2015). At this time, we do not have the amount and type of data needed for a deeper understanding of species richness along the studied elevational gradient.

Table 3. Compilation of the results from different studies on tree assemblages analyzing the relationships between species richness and elevation (A, B), phylodiversity and elevation (A), family age and elevation and / or latitude (B). The datasets of the studies differed: Some studies included gymnosperms and some excluded gymnosperms (column G). Denoted are the observed patterns (increase (+), decrease (-) or hump-shaped (hump) of species richness, phylodiversity and age) in relation to increasing elevation or increasing latitude.

A	Study	Study area	G	Species richness ~ elevation	Phylodiversity ~ elevation	
	Bryant et al. (2008)	USA	No	hump	hump	
	Tallents et al. (2005)	Tanzania	Yes	no pattern	+	
	Culmsee and Leuschner (2013)	Malesia	Yes		+	
	Dossa et al. (2013)	Indonesia	Yes		-	
	Qian et al. (2014)	China	No	-	-	
B					Age ~ elevation	Age ~ latitude
	Segovia et al. (2013)	Chile	No	-		+
	Qian (2014)	South America	No	-	+	-

Phylodiversity

Assuming PNC we expected to find phylogenetically diverse assemblages at low elevations and a decrease in phylodiversity with increasing elevation, comparable to results from a tropical volcano in Indonesia (Dossa et al. 2013). However, in contrast to these predictions we found no significant changes of the tip level phylodiversity and an increase in phylodiversity with elevation for the clade-level metric of phylodiversity. These results are in agreement with findings by Tallents et al. (2005) and Culmsee and Leuschner (2013), who analyzed the clade level phylodiversity of tree assemblages (including angiosperms and gymnosperms) in Tanzania and Malesia (see Table 3). Tallents et al. (2005) explain the high phylodiversity at high elevations by the presence of gymnosperms. Our findings support the results of this previous study, as we found gymnosperm species only within the mid and high elevation plots even though the gymnosperms were not among the most common species (see Table 1). The importance of gymnosperms is also emphasized by the fact that we detected a positive trend between phylodiversity and elevation at the clade level (sesMPD) but not at the tip level (sesMNTD). Gymnosperms originated during the Carboniferous around 319 mya (Beck 1966, Galtier and Rowe 1989) – long before the ancestral line of angiosperms originated in the Jurassic around 160 mya (De Bodt et al. 2005).

We detected no relationship between both phylodiversity measures and elevation when considering only angiosperms. In contrast to our results, previous studies showed that phylodiversity of angiosperms in the Rocky Mountains was hump-shaped with highest diversities at 3000 m a.s.l. whereas phylodiversity of angiosperms in China decreased with elevation (Bryant et al. 2008, Qian et al. 2014; see Table 3). Our finding (no relationship of angiosperm phylodiversity with elevation) and the finding from the Rocky Mountains (increasing angiosperm phylodiversity up to 3000 m a.s.l.) contradict the idea that the importance of environmental filtering increases with elevation (Hardy et al. 2012, Qian et al. 2014). Overall, our results of the phylodiversity analysis emphasize the role of gymnosperms in affecting phylodiversity along the elevational gradient, although gymnosperms had low abundances.

Family age

Mean family age and clade level phylodiversity of tree assemblages were significantly and positively correlated across plots irrespectively of whether we used presence-absence or abundance based metrics. This suggests that the phylodiversity and mean family age, which we used in our analysis, were not influenced by the distribution of abundances within plots. However, angiosperm assemblages containing species from old clades were not per se phylogenetically more diverse, which underlines that these two metrics –while using similar data sets – measure independent characteristics of the assemblages.

The observed values and the standardized effect sizes of the mean family age of our tree assemblages (including or excluding gymnosperms) increased with elevation. These findings contradict predictions according to PNC and latitudinal patterns species from younger clades were often found at higher latitudes (Hawkins et al. 2003, 2011, Jansson et al. 2013, Qian et al. 2013, Kerkhoff et al. 2014). In our study, gymnosperms were not the only driver of the increase in mean family age along the elevational gradient. While species from old families (up to the maximum family age of 143.8 my) occurred across the whole range of the elevational gradient with highest abundances at mid and high elevations (Supplementary Figure 2.2 in Appendix), species within the youngest families (25.2 myr to 36 myr) did not occur in the high elevation plots and were most abundant in the low elevation plots (Supplementary Figure 2.2 in Appendix). Therefore, our results are in line with two recent studies from South America that also found increases in mean family ages with increasing elevation and increasing latitude for assemblages of angiosperm trees, thus, contradicting the PNC (Qian 2014; Segovia et al. 2013; see Table 3). Qian (2014), Segovia and Armesto (2015) and Segovia et al. (2013) proposed that the occurrence of elements from old floras with extra-tropical origins in high elevation habitats causes higher average family ages of the tree assemblages. In addition, Segovia and Armesto (2015) pointed out that the flora at 40 °S latitude in southern South America is dominated by Australasian and Austral-Antarctic elements (Kerkhoff et al. 2014). The Andean uplift during the Neogene created more temperate habitat at higher elevations and could have allowed the northward migration of Gondwanan taxa into tropical latitudes along the

slopes of the mountains (Segovia and Armesto 2015). Our results support this idea as the historical origins of most of the oldest tree families (> 100 myr) were located on the Gondwanan landmass (Raven and Axelrod 1974; see Table 1) and macrofossils from Podocarpus have been reported from the Paleocene (~ 60 mya) of Patagonia (Morley 2011). We consequently suggest that the immigration of ancient lineages with Gondwanan origins into South America and their subsequent migration along the rising high elevation habitats has influenced the species composition of tree assemblages along the Andean slopes. Our study revealed that evolutionary patterns of Andean tree assemblages are more distinct when measures consider the phylogenetic structure deep within the phylogeny of plants. Generally, the observed elevational patterns of the three different measures (MNTD, MPD and mean family age) of the phylogenetic or evolutionary history got stronger the further these measures accessed deeper nodes of the phylogeny. The MNTD reflects patterns at the tip level, the MPD reflects patterns at the clade level, whereas family age is driven by the relatively deep family nodes in the phylogeny.

Conclusion

Patterns of species richness, phylodiversity, and mean family age for tree assemblages along the studied elevational gradient in the tropical Andes contradict the phylogenetic niche conservatism (PNC). We could show that two gymnosperm species that occur on high elevation habitats of the Andes strongly influence the pattern of increasing phylodiversity with elevation. Importantly, we found that average family ages of tree species increased along the elevational gradient and this increase was not merely driven by the occurrence of gymnosperms at high elevations. To this end, we suggest that the dispersal of evolutionarily ancient lineages into the tropical Andes was one important process affecting the current composition of tree assemblages along elevational gradients in the Andes. Our results highlight that PNC does not necessarily drive patterns of tree assembly along elevational gradients in Ecuador, but that the biogeographical history of the Andes may play a more important role for today's composition of tree assemblages. To obtain more definitive conclusions, we recommend further studies using broader elevational gradients and more highly resolved phylogenies to estimate family and species ages.

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Chapter 3

Beyond body size: Consistent decrease of traits within orthopteran assemblages with elevation

with
Claudia Hemp | Antje Schmidt | Thomas Nauss |
Roland Brandl | Nina Farwig |

submitted to Ecology

Summary

Morphological traits provide the interface between species and their environment. For example, body size affects the fitness of individuals in various ways and is known to increase in endotherms with decreasing temperature, known as Bergmann's rule. Especially for ectotherms, the applicability of general rules of interspecific clines of body size and even more so of other morphological traits is still under debate. Here we tested relationships between elevation (as a proxy for temperature) and productivity and four ecologically relevant morphological traits of orthopteran assemblages that are related to fecundity (body size), dispersal (wing length), jumping ability (hind femur length), and predator detection (eye size). We measured traits of 160 orthopteran species that were sampled along an extensive environmental gradient at Mt. Kilimanjaro (Tanzania), spanning elevations from 790 to 4,410 m a.s.l. with different levels of plant productivity. Bayesian analyses revealed that interspecific body size, relative wing length, hind femur length, and eye size of orthopteran assemblages decreased with increasing elevation. Body size and relative eye size also decreased with increasing productivity. Our results suggest that orthopteran assemblages had higher fecundity, better dispersal and escape abilities, and better predator detection at higher temperatures (low elevations), than at low temperatures (high elevations). Large body sizes might be advantageous in habitats with low productivity because of a reduced risk of starvation. Likewise, large eye size might be advantageous because of the ability to detect predators in habitats with low vegetation cover, where hiding possibilities are scarce. Our study highlights that changes in temperature and productivity not only lead to interspecific changes in body size, but are also related to independent changes of other morphological traits that influence the ecological fit of organisms in their environment.

Introduction

Species are characterized by a unique set of morphological, physiological, and behavioral traits (De Queiroz 2007). These traits influence the fitness of individuals (McGill et al. 2006, Violle et al. 2007, Webb et al. 2010, Nock et al. 2016) and provide the basis for interactions between species and their abiotic and biotic environment. The most important trait influencing animal fitness (LaBarbera 1989) is body size. According to Bergmann's rule, species of larger size are found in colder environments, and those of smaller size are found in warmer environments (Bergmann 1847), but the generality of body size clines of both endotherms and ectotherms along latitudinal and elevational gradients is intensively debated (Watt et al. 2010, Shelomi 2012). In arthropods, important interactions have been identified not only between body size, fecundity, and thermoregulation (Whitman 2008), but also between wing length and dispersal ability (Picaud and Petit 2008), hind femur length and escape ability (Queathem 1991), and eye size and predator detection (Land 1997). The composition of species, body sizes, and other morphological traits is therefore influenced by both abiotic and biotic factors (Bässler et al. 2016, Nock et al. 2016, Schellenberger Costa et al. 2017) and will consequently change if these factors are anthropogenically changed. This will lead to critical impacts on species interactions and ecosystem functioning (Millien et al. 2006, Webb et al. 2010, Ohlberger 2013).

Orthoptera (grasshoppers, bush crickets, and crickets) is an abundant and species-rich order that occurs from sea level up to almost 5,000 m a.s.l. (Alexander 1951, Bidau 2014). Differences in the composition of morphological traits of orthopterans, such as body size and wing length, have been related to changes in abiotic and biotic factors along environmental gradients (Hodkinson 2005). Along elevational gradients, one of the most striking patterns is the almost linear decline in temperature (Körner 2007), which is one of the most important factors for ectothermic animals (Zeuss et al. 2017) like orthopterans. At high elevations, low temperatures lead to low food availability, and short growing seasons reduce the period for larval development. Orthopterans must therefore complete their full life cycle within a single season (Berner et al. 2004). Fast development is related to small adult body sizes (Abrams et al. 1996, Berner et al. 2004). By contrast, in habitats with high temperatures and extended growing seasons, e.g., at low elevations, orthopterans should have a larger body size, which has positive effects on fecundity, thermoregulatory ability, and desiccation resistance (for a comprehensive review on the significance of orthopteran body size, see Whitman 2008). The atmospheric pressure,

which similarly decreases with increasing elevation, can also influence morphological traits. At high elevations, low atmospheric pressure combined with low temperatures hampers the flight performance of insects (Dillon et al. 2006). Consequently, insects in high elevation habitats often have partly reduced wings (brachyptery) or completely reduced wings (aptery; (Alexander 1951, Sømme 1989). The relationships between morphological traits and environmental factors are dynamic and complex, elevational clines in body size depend on the studied taxon, and patterns might differ at intraspecific and interspecific scales (Shelomi 2012).

Biotic factors, such as resource availability, are also important for the composition of assemblages in respect to morphological traits (Lavorel and Garnier 2002, Clapham and Karr 2012). For example, food quality positively influences growth rates and fecundity of grasshoppers within species (Fielding 2004). Resource availability should also be of importance at interspecific scales. Enhancements or enlargements of morphological traits often demand additional energy for structural reinforcements, e.g., of the muscular system or the exoskeleton (Zera and Denno 1997, Belovsky 1997, Whitman 2008). A useful measure of resource availability for herbivorous species such as orthopterans is plant productivity (Wolverton et al. 2009). In accordance with the resource availability hypothesis, areas with high productivity can provide habitat for assemblages of orthopterans with traits that require more resources, e.g., large body size (Huston and Wolverton 2011, Van der Plas et al. 2012). However, also habitats with sparse, variable, or unpredictable resources can favor resource-intensive traits, such as those that increase dispersal ability (Roff 1990, Denno et al. 1991, Zera and Denno 1997). For example, long wings are resource intensive but increase flight ability and are beneficial for tracking resources and colonizing new habitats (Denno et al. 1991, Picaud and Petit 2008). Traits related to mobility are relevant not only for dispersal, but also for escaping from predators. The ability of orthopterans to escape is positively influenced by the length of the hind legs (Picaud and Petit 2007). Flying insects escape predators mainly because of the initial acceleration, which is linked to the length of the hind leg (Queathem 1991) and especially to the length of the hind femur, which contains major muscles of the hind legs (Bennet-Clark 1990). Long hind legs increase the ability to launch the body into flight, to move further away from the predator, and to jump from less stiff substrates (Queathem 1991, Dudley 2002, Burrows and Sutton 2008). The ability to reduce predation risk is additionally affected by behavioral and sensory traits (Bucher et al. 2014). Orthopterans use a variety of mechanical, chemical, acoustic, and visual cues to detect predators (Steiner 1981 and references within, Dangles et al. 2005). For instance, the sensory system of grasshoppers allows them to adapt their escape distance and angle in response to the speed and direction of approaching predators (Cooper 2006). The eye size is thereby positively related to the size of the visual field and to the overall vision acuity and sensitivity, and thus positively affects the ability to visually detect predators (Land 1997, Rutowski 2000). The visual system of phytophagous insects even allows them to differentiate species of host plants (Reeves 2011). However, other factors, such as the ability to hide, camouflage color, and predator pressure, will also influence anti-predator traits of orthopterans (Belovsky and Slade 1993, Eterovick et al. 1997, Branson 2005, Whitman 2008).

Despite intensive studies of intraspecific and interspecific patterns of body size across environmental gradients (Millien et al. 2006, Shelomi 2012), the applicability of general rules, especially on interspecific body size clines of ectotherms, is still under debate (Atkinson 1994, Blanckenhorn and Demont 2004, Shelomi 2012, Zeuss et al. 2017). Little is known about changes in the composition of assemblages in respect to other morphological traits along environmental gradients. Here, we examined how changes in elevation (as a proxy for temperature changes) and productivity influence morphological traits of orthopteran assemblages that are related to fecundity (body size), dispersal (wing length), jumping ability (hind femur length), and predator detection (eye size). We used an extensive dataset from 440 study plots of 160 orthopteran species collected within 14 years along a steep elevational gradient ranging from 790 to 4,410 m a.s.l. on the slopes of Mt. Kilimanjaro (Tanzania). We hypothesized that areas at high elevations with low temperatures, short activity periods, and low atmospheric pressure should favor fast development, small body sizes, and short wings of orthopteran assemblages. We also expected that high productivity favors orthopteran assemblages with resource intensive traits that can benefit fecundity, dispersal ability, escape ability,

and predator detection. We used simple Bayesian inference to test the following two main predictions: (1) body size, wing length, hind femur length, and eye size of orthopteran assemblages decrease with increasing elevation, i.e., with decreasing temperature, and (2) body size, wing length, hind femur length, and eye size of orthopteran assemblages increase with increasing productivity.

Methods

Study area

We conducted the study along the slopes of Mt. Kilimanjaro in northeastern Tanzania. At low elevations (700–1,000 m a.s.l.), the study area is characterized by savanna woodland and grassland that has almost completely been converted to agricultural lands. The sub-montane zone between 1,000 and 1,500 m a.s.l. is characterized by complex multi-cropping agroforestry. The next higher zones consist of lower and middle montane forest (1,500–2,500 m a.s.l.), upper montane forest (2,500–3,500 m a.s.l.), and sub-alpine forest zone of heathlands and cushion vegetation (~ 3,700 m a.s.l.). Elevations above 4,500 m a.s.l. are practically bare of vegetation. Precipitation follows the intertropical convergence zone modified by elevation (Hemp 2006), with one rainy season between March and May and another between October and November (Maeda and Hurskainen 2014). The mean annual land surface temperature decreases with elevation from 20.2 °C at lower elevations (1,500–2,000 m a.s.l.), to 12.6 °C at mid-elevations (2,000–3,000 m a.s.l.), to 8.5 °C at high elevations (above 4,000 m a.s.l.; Maeda and Hurskainen 2014), with a typical moist adiabatic lapse rate of around −0.56 K per 100 m (Hemp 2006). Anthropogenic disturbance comprises agriculture involving fertilizer and herbicide applications in lowland areas, and fires, occasional timber extraction, and collection of forest products at higher elevations (Hemp and Hemp 2003).

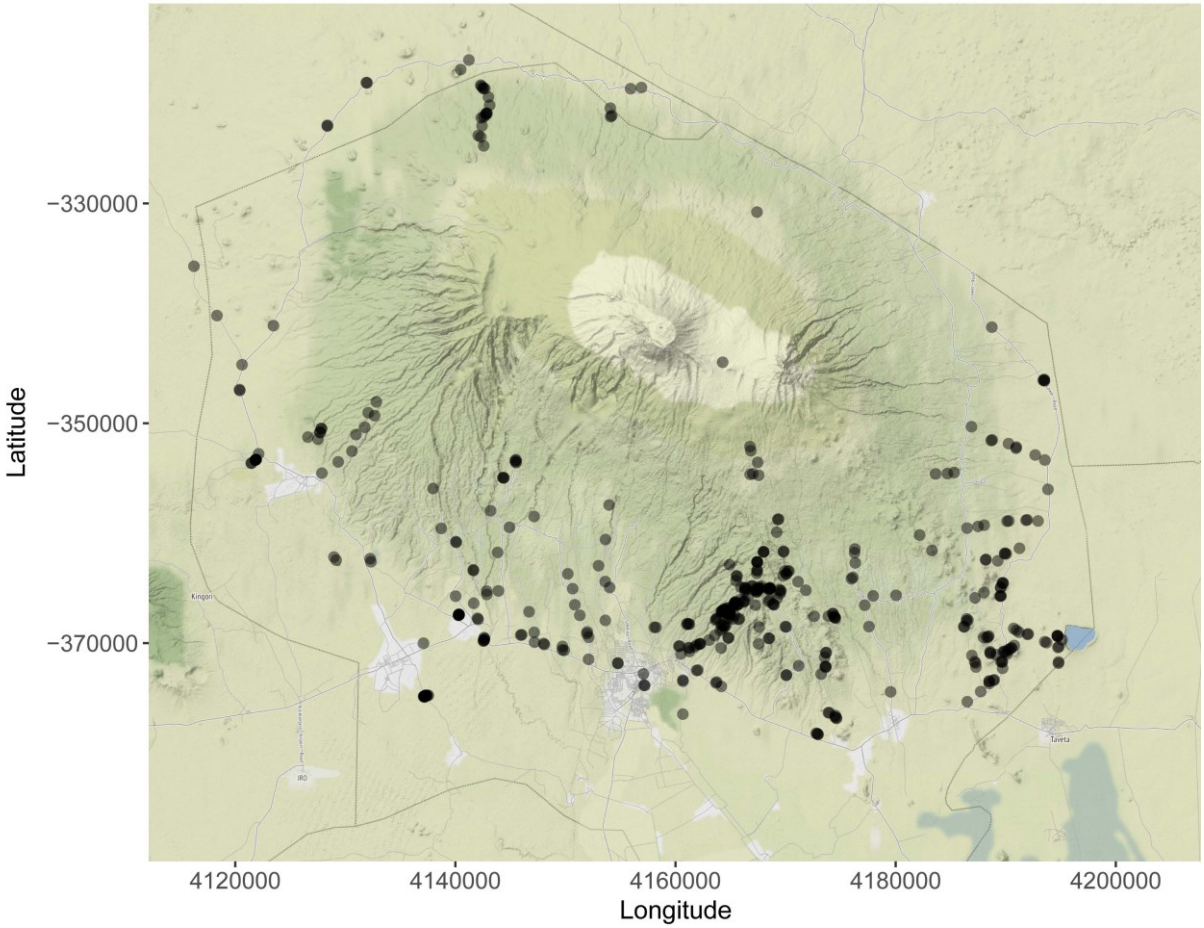

Figure 1. Study area around Mt. Kilimanjaro in northeastern Tanzania. Gray dots depict location of 440 study plots, close-by plots that overlap on the map appear black. Map tiles by Stamen Design, licensed under CC BY 3.0. Data by OpenStreetMap, licensed under ODbL.

Sampling of orthopterans

The abundance and density of orthopteran species on 440 study plots in open and forest habitats along an elevational gradient from 790 to 4,410 m a.s.l (Fig. 1) were recorded by CH yearround over 14 years (1996–2012); most of the plots were located in the lower areas of the gradient between 790 and 2,280 m a.s.l. Each plot (30 x 30 m^2) was sampled one to six times, except for four plots, which were sampled 23, 25, 45, and 47 times, respectively, yielding a total of 736 samplings.

The abundance of orthopteran species was estimated on the basis of sighted individuals and singing males. The observer (CH) strode through each plot on ten parallel transects of 3 m distance during the day and at night and recorded all species seen and heard. Where present, shrubs and trees were shaken to search for tree-dwelling species. The abundances were assigned to five categories according to Hemp and Hemp (2003): (1) 1 individual in the plot, (2) < 1 individual/m^2, (3) ca. 1 individual/m^2, (4) ca. 5 individuals/m^2, and (5) > 5 individuals/m^2.

Estimating productivity

We used the normalized difference vegetation index (NDVI) as an estimate of productivity, as often used in ecological studies (Oindo 2002, Kerr and Ostrovsky 2003, Wallis et al. 2017, Röder et al. 2017). NDVI is a measure of greenness calculated from reflectance in the near-infrared and red portions of the electromagnetic spectrum. The NDVI uses differences in the reflectance to distinguish between full vegetation cover (NDVI = +1) and waterbodies (NDVI = −1). We generated NDVI values from the cloud-free and terrain-corrected Landsat GLS 2000 data collection (see https://landsat.usgs.gov/global-land-surveys-gls) at a 30 m resolution for each plot. NDVI values ranged from −0.33 to 0.58 (0.038 ± 0.21; mean ± SD) and showed a hump-shaped pattern, with highest values at mid-elevations around 2000 m a.s.l. (Supplementary Figure 3.1 C in Appendix); this pattern resembles the elevational pattern of precipitation which, on the southern slopes of Mt. Kilimanjaro, also peaks at mid-elevations (Hemp 2006).

Processing of traits

We measured ten continuous morphological traits of 657 individuals of 160 orthopteran species, namely body length, pronotum length, pronotum width, wing length, length of the femur of the front, middle, and hind legs, length of the tibia of the hind leg, eye diameter, and interocular distance. The ten traits are important components of the body size and overall morphological shape of insects and are linked to abiotic and biotic factors (e.g., productivity) as described in the introduction. We measured the traits of one to four male and female individuals of each species, depending on the number of individuals sampled (males of eight species were not found, and females of two species were not found). For some individuals, we could not obtain measurements of each trait: values were lacking for the interocular distance of two individuals, length of front leg femur of six individuals, length of middle leg femur of four individuals, length of hind leg femur of seven individuals, and length of hind leg tibia of ten individuals. In these cases, we replaced the missing value by the mean trait value of the same species and sex. We then calculated the mean trait value of each sex and species and the mean trait value for each species.

The four traits body size, wing length, hind femur length, and eye size are related to the functional aspects fecundity, dispersal, jumping ability, and predator detection, respectively (see Introduction). Before we calculated the community-weighted mean (CWM) values of the four traits, we preprocessed the original trait measures. To obtain a general estimate of total body size, we calculated a multivariate measure across the ten traits. This method is preferred over univariate measures because it is more likely to accurately reflect the overall size, especially when working with taxa from different families (Green 2001). We first $\log_{10}$-transformed all trait measures. For wing length, we used square root transformation because of the occurrence of zeros (O'Hara and Kotze, 2010). We then conducted a principal component analysis based on the covariance matrix of the ten traits using the function prcomp implemented in the R Stats Package (R Core Team 2017). We extracted the species scores along the first axis and used these as multivariate measures of species body size. Wing length, hind femur length, and eye size covary with body length. We therefore corrected the measures of the three traits for covariance with body length by using residuals of linear regressions of the trait values plotted against body length (relative traits; Stern and Emlen 1999). We

then calculated the CWMs of the multivariate body size and the three relative trait measures with the function functcomp from the R package FD (Laliberté et al. 2014). The CWM values reflect the mean trait value of all species in the assemblage weighted by their relative commonness. Patterns of changes of CWM trait values can be contrary to patterns of unweighted average trait values across species when overall abundances of species with large or small traits increase or decrease (see discussion in Schellenberger Costa et al. 2017). We therefore additionally calculated the unweighted community mean of trait values, where we treated the trait values of each species equally (mean of species present). In the following, we used the CWM values of the four preprocessed traits in linear regressions against environmental measures.

Following Zelený and Schaffers (2012), co-occurrence of species can lead to internal statistical relationships of no biological significance, e.g., when trait values are generated at the assemblage level by assigning values to species and averaging them at the plot level. To correct for this potential bias, we used a permutation method with standardized effect sizes proposed by Zelený and Schaffers (2012) and tested whether the CWM trait values differed from values expected under a random trait distribution. This permutation method corrects for inflated Type I error. Differences between observed patterns and random patterns from null models indicate that ecological processes structured the observed pattern. However, there is still no methodological solution to the problem that co-occurrence of species and covariation of variables with species richness could still lead to spurious correlations and biased regression coefficients (Hawkins et al. 2017). For the null model, we randomized the rows of the species traits matrix 1000 times, while keeping the trait combinations fixed (random trait combinations are not biologically meaningful). This null model leads to orthopteran assemblages with random trait syndromes. Afterwards, we calculated standardized effect sizes (ses) for the CWM trait values as ses $X = [X_{observed} - mean(X_{random})]/SD(X_{random})$, where $X_{observed}$ is the observed CWM trait value, mean (X_{random}) is the mean of the randomizations of the null model, and SD (X_{random}) is the standard deviation of the randomly calculated CWM trait value.

Evolutionary or physical constraints can lead to disproportionate changes in morphological traits (L) with body size B ($L \propto Bb$; see Shingleton et al. 2007 for an overview of allometric relationships). Morphological traits scale isometrically when $b = 1$, hypometrically when $b < 1$, and hypermetrically when $b > 1$. Allometry of traits with body size can therefore lead to constrained relationships of trait values with environmental factors if body size correlates with the environmental factor. Hypermetry of wing length with body size (larger orthopterans have proportionally larger wings) could lead, e.g., to a negative relationship of wing length with increasing elevation if body size decreases with elevation. We therefore tested for evolutionary allometry within orthopteran species by calculating the scaling exponent (b) of the $\log_{10}$-transformed traits wing length, hind femur length, and eye size to $\log_{10}$-body length. To do so, we used the function ma from the R package smatr (Warton et al. 2012). Significance of deviations from isometry was evaluated by calculating 95% confidence intervals for the regression slopes. The relationship between wing length and body length was hypermetric because 40 species had very short wings. When we excluded these 40 species from the data set, the relationship was isometric (Supplementary Figure 3.2 A, B and Table 3.1 in Appendix). For hind femur length and eye size, b did not differ significantly from one, which indicated isometry with body length (Supplemtary Figure 3.2 C and D, Supplementary Table 3.1 in Appendix). We therefore expected that patterns in trait changes along environmental gradients are not driven by scaling relationships.

Effects of abiotic and biotic factors on traits

We used Bayesian linear mixed models to test the effects of elevation and NDVI on the CWM values, the unweighted community mean values, and on the standardized effect sizes of the CWM values of the four preprocessed (for details, see previous section) morphological traits body size, wing length, length of hind femur, and eye size. We used a normal error distribution and fitted all models using Markov-Chain-Monte-Carlo sampling and the Stan program (Carpenter et al. 2017) in the RStanArm library (function stan_lmer; Stan Development Team 2016) in the R statistical environment (R Core Team 2017). To correct for the nested structure of our data (data from different months and years) and for pseudo-replication (data were collected several times on the same plots), we included sampling

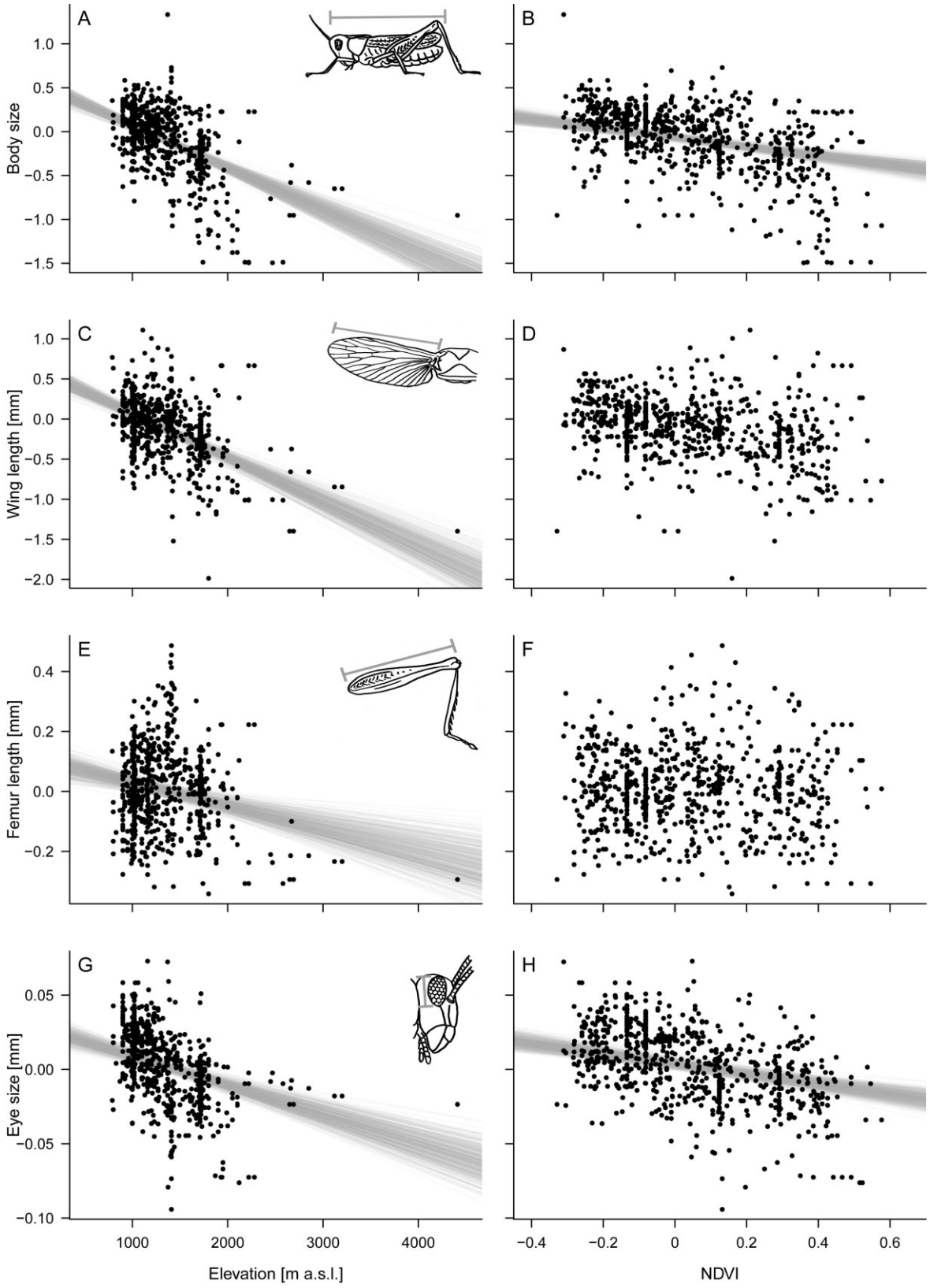

Figure 2. Patterns of community weighted mean (CWM) values of body size (A, B), wing length (C, D), hind femur length (E, F), and eye size (G, H) with increasing elevation (A, C, E, G) and with increasing normalized difference vegetation index (NDVI) (B, D, F, H). Body size was calculated as the species score from a multidimensional analysis of nine orthopteran traits (for details, see Methods section). Other CWM trait values are measures relative to body length and are calculated as the residues of a linear model of the trait values plotted against body length. Positive trait values therefore indicate values that are higher than expected from the body length; negative values indicate lower values than expected. Lines indicate significant relationships, where each line represents one posterior sample mean. Dots depict underlying raw data from 440 study plots.

Table 1. Effects of elevation and NDVI on four traits of orthopteran assemblages derived from Bayesian linear mixed models.

Parameter	Mean	SD	CI 2.5%	CI 97.5%
Model 1: body size				
Intercept	**−0.087**	0.020	−0.13	−0.048
Elevation	**−0.18**	0.016	−0.21	−0.15
NDVI	**−0.11**	0.016	−0.14	−0.075
Model 2: wing length				
Intercept	**−0.11**	0.028	−0.17	−0.057
Elevation	**−0.21**	0.017	−0.24	−0.17
NDVI	−0.031	0.017	−0.064	−0.0036
Model 3: hind femur length				
Intercept	0.0040	0.012	−0.018	0.028
Elevation	**−0.029**	0.0068	−0.042	−0.015
NDVI	0.0045	0.0064	−0.0082	0.017
Model 4: eye size				
Intercept	0.0024	0.0019	−0.0013	0.0061
Elevation	**−0.0073**	0.0010	−0.0093	−0.0053
NDVI	**−0.0070**	0.0010	−0.0090	−0.0049

Notes: Month of sampling nested in sampling year and study plot were included as two random effects in all models. Predictors were standardized to zero mean and unit variance to ease the comparison of effect sizes. Trait values for the CWM calculation of models 2, 3, and 4 were residuals of linear regressions of the trait values plotted against body length. Models were fitted using normal error distribution. Mean: mean estimate (intercept) or mean slope (predictor) of the 4,000 samples; SD: standard deviation; CI: credible interval; intercept: response value at mean elevation and mean normalized difference vegetation index (NDVI). Boldface indicates posterior estimates of predictor variables with significant effects on the model response (CI does not include zero).

month nested in year, as as well as the study plot as two random effects in all models. To allow for comparison of the model coefficients of the fixed effects, we applied a z-transformation to all predictor variables. All coefficient and variance parameters were given uninformative prior distributions [intercept ~N(0, 10); coefficients ~N(0, 2.5)]. To keep the parameters scale free, the priors were additionally scaled internally by multiplying the prior by 2 * SD (predictor). Mismatches of the scales of the sampler resolution and the target distribution can lead to divergent transitions and biased estimates of the posterior distribution. Owing to the occurrence of divergent transitions, we adjusted the sampler resolution for the models of wing length, hind femur length, and eye size by setting the target acceptance probability of 0.95 to 0.99. This leads to smaller step sizes of the sampler and decreases approximation error. The Markov-Chain-Monte-Carlo implementation used four chains of 2,000 iterations; the first 1,000 iterations in each chain were discarded as burn-in to achieve convergence, which resulted in 4,000 samples for each posterior distribution. Chain convergence and autocorrelation were assessed using trace plots of posterior samples. The values of the Gelman-Rubin statistic (the potential scale reduction factor from the comparison of within-chain variance and between-chain variance) indicated convergence with $\hat{R} < 1.1$ for all parameters in all models.

We are aware that the distribution of plots along the studied gradient was unbalanced, with 11 plots (1.5%) distributed across 58% of the elevation gradient (from 2300 to 4410 m a.s.l.) and 437 plots (98.5%) covering the lower part of the gradient (from 790 to 2300 m a.s.l.). We therefore

tested whether the observations at plots higher than 2300 m a.s.l. influenced the pattern of morphological traits. For this, we conducted all Bayesian linear mixed models with a dataset in which we excluded data from plots higher than 2300 m a.s.l. (11 observations from 11 plots) using the same approach as described above.

Results

In total, we recorded 160 orthopteran species across 448 study plots. These species belonged to 114 genera from 9 families (Acrididae, Euschmidtiidae, Gryllacrididae, Lentulidae, Pamphagidae, Pyrgomorphidae, Tetrigidae, Tettigoniidae and Thericleidae). Species richness ranged from 0 to 27 species (Supplementary Figure 3.1 A in Appendix for the variation of species richness along the elevational gradient). The original trait values ranged from 0 (without wings) to 6.4 mm for wing length, from 0.56 to 4.4 mm for hind femur length, and from 0.07 to 0.48 mm for eye diameter (Supplementary Table 3.2 in Appendix; also for the residuals of linear regressions of the trait values plotted against body length). The first axis of the principal component analysis of the ten morphological traits explained 75% of the trait variation (Supplementary Figure 3.3 and Supplementary Table 3.3 in Appendix). The multivariate body size measure ranged from −1.62 to 1.69 (± 0.75 SD) and was positively correlated with the measured body length ($r^2 = 0.80$, $p < 0.005$; Pearson's product-moment correlation coefficient).

Species richness decreased with increasing elevation (Supplementary Figure 3.1 and Supplementary Table 3.4 in Appendix). Likewise, CWM values of the four traits body size, wing length, hind femur length, and eye size decreased with increasing elevation (Table 1; Fig. 2). The patterns were also significant for standardized effect sizes of the four CWM trait values (Supplementary Figure 3.4; Supplementary Table 3.5 in Appendix). The CWM values of body size and eye size as well as their standardized effect sizes were negatively correlated with NDVI (Table 1; Fig. 2 for CWM values, Supplementary Figure 3.4 and Supplementary Table 3.5 in Appendix for standardized effect sizes). Wing length and NDVI were negatively related when standardized effect sizes were used (Supplementary Figure 3.4 and Supplementary Table 3.5 in Appendix). The relationships between elevation or NDVI and the morphological traits were not significant when we used unweighted community mean trait values or their standardized effect sizes, except for the relationship between eye size and NDVI (Supplementary Figure 3.5 and 3.6 in Appendix). This indicates that the patterns of CWM trait values are driven by changes in the abundance of species and not by changes in the presence of species along the studied gradients. The Bayesian linear mixed models with a reduced data set (excluding plots higher than 2300 m a.s.l.) revealed similar results for body size, wing length, and eye size compared to the analyses using all data (Supplementary Figure 3.7 and Supplementary Table 3.6 in Appendix). Only the relationship between elevation and hind femur length was not significant when the reduced data set was used (Supplementary Figure 3.7 and Supplementary Table 3.6 in Appendix). In the discussion, we will only refer to patterns that resulted from CWM trait values of the complete data set.

Discussion

Our study revealed a clear negative relationship between elevation and body size of orthopteran assemblages. Independently from the body size pattern, the relative wing length, hind femur length, and eye size also decreased with increasing elevation (traits were corrected for covariance with body length). In addition, productivity (measured as NDVI) was negatively related to body size and eye size.

Effects of environmental factors on body size

The body size of orthopteran assemblages decreased with increasing elevation. This finding is in line with the general pattern of decreasing body sizes of ectotherms towards colder areas (Janes 1994, Whitman 2008, Parsons and Joern 2014, but also see Zeuss et al. 2017). For instance, body sizes of bees decrease with increasing elevation at Mt. Kilimanjaro (Schellenberger Costa et al. 2017). Likewise, body sizes of grasshopper assemblages decrease with increasing elevation in the Cantabrian Mountains in Spain, even though the pattern is stronger at the intraspecific scale than at the interspecific scale (Laiolo et al. 2013). Decreasing insect body sizes with increasing elevation are often explained by the decreasing season length, which favors fast development (Blanckenhorn and Demont 2004, Parsons

and Joern 2014, but also see Zeuss et al. 2017). In contrast to these patterns, Schellenberger Costa et al. (2017) found increasing body sizes of moths at Mt. Kilimanjaro with increasing elevation and explained their finding with benefits of efficient energy use of large individuals under harsh environmental conditions at high elevations. Nevertheless, the growing season at Mt. Kilimanjaro starts to be limiting only at elevations higher than 2,700 m a.s.l. (Hemp 2006) and is therefore not likely to be the reason for the observed pattern in our study area. Instead, we propose that the declining temperature with increasing elevation is the main driver of the observed pattern. Decreasing temperature negatively affects temperature-dependent biochemical processes and growth rates (van der Have and de Jong 1996), and low temperature shortens the larval growth period via a hormonal pathway that leads to small adult body size (Chown and Gaston 2010). Large orthopteran species, by contrast, have advantages in warm habitats at low elevations, namely reduced desiccation risk (Chown and Gaston 2010). Large size reduces the rate of water loss owing to the smaller surface-to-volume ratio and simultaneously increases the capacity to store water (Chown and Gaston 1999 and references within). Furthermore, large size is advantageous for effective thermoregulation; overheating is prevented because a high thermal inertia of high body mass relates to greater temperature homeostasis (Whitman 1987). However, effective thermoregulation would also be beneficial at high elevations where temperatures are low and can be also influenced by cuticle color (Bishop et al. 2016). This might explain why we did not find the smallest orthopteran assemblages on plots at the highest elevations.

We used the NDVI as a measure of productivity and as a proxy for resource availability. The NDVI values along our studied environmental gradient indicated the highest productivity at mid-elevation. At this elevation, temperature is favorable for plant growth and humidity reaches its maximum, which allow submontane and lower montane forests to grow (Hemp 2006). In line with the resource availability hypothesis, we expected positive relationships between productivity and the four morphological traits because of positive effects of the traits representing fecundity, dispersal ability, jumping ability, and predation risk. The finding of decreasing body sizes of assemblages with increasing productivity therefore contrasts our expectation. However, large body size not only increases fecundity of orthopterans, for example, but also their starvation resistance (Whitman 2008). High resistance to starvation would be of particular advantage in habitats with low productivity. Furthermore, large orthopteran species have a wide dietary breadth and are able to chew tough food, which makes them both intraspecifically and interspecifically competitive (Fielding 2004, Whitman 2008). Large size might therefore be particularly advantageous at low elevations, where starvation risk is high.

Effects of environmental factors on wing length

In accordance with our expectation, the relative wing length of orthopteran assemblages decreased along the elevational gradient. We used residuals from linear models of the trait values plotted against body length as trait measures because morphological traits usually scale with body length. The significant negative relationship between wing length and elevation therefore indicates that wing length decreases more strongly than expected from the decrease in body length. The reduction or loss of wings is a common adaptation of insects at high elevations (Hodkinson 2005). Low air density at high elevation hampers flight performance of insects. Furthermore, low temperatures at high elevation additionally lead to low metabolic rates and negatively affect muscle physiology (Dillon et al. 2006 and references within). The maintenance of flight performance at high elevations by means of, e.g., increasing wing length or wing area would therefore be exceptionally resource intensive (Dillon et al. 2006).

Contrary to our expectation, wing length of orthopteran assemblages did not respond to changes in productivity. However, our analysis of the pattern of standardized effect sizes of wing length revealed a significant but negative relationship to productivity. Even though the maintenance of long wings is resource intensive, benefits of long wings, especially in areas with low productivity, might counterbalance the costs. Long wings increase flight ability, which provides advantages for resource tracking, colonization of new habitats, and finding of mates. Short wings and winglessness, by contrast, are a common local adaptation to long-term stable habitats (Roff 1990, Denno et al. 1991, Zera and Denno 1997, Picaud and Petit 2008). However, the NDVI measure does not incorporate habitat

stability, temporal variability, or the distribution of resources in adjacent areas. This might explain why we did not find a significant pattern for the original pattern of wing length with productivity.

Effects of environmental factors on hind femur length and eye size

Hind femur length and eye size (corrected for covariance with body length) also decreased with increasing elevation. Both traits influence the ability to avoid predation. Hind femur length is positively related to the ability to jump and therefore affects escape ability, whereas eye size positively affects the quality of the visual system, which influences predator detection (Bennet-Clark 1990, Rutowski 2000). Our results therefore suggest that orthopteran assemblages have better anti-predator traits at low elevations than at high elevations. However, note that elevation explained only a relatively small portion of the variation in hind femur length, and the pattern was mainly driven by assemblages at the high elevation plots that were characterized by few species with relatively short legs. Changes in predation pressure along the elevation gradient might be a possible explanation for the decrease in hind femur length and eye size with increasing elevation (Roslin et al. 2017). Birds and spiders are the main predators of orthopterans, and their abundances generally decline with increasing elevation, often with mid-elevation peaks (Rahbek 1995, Branson 2005, Röder et al. 2017). We do not have data on predator abundances on our plots, but we speculate that assemblages of orthopterans in areas with more predators would consist of more species with long hind femurs and large eyes because of the benefits of enhanced escape ability and predator detection. Another possible explanation for the decrease in eye size with increasing elevation is the increasing UV radiation. High UV radiation can damage the visual system of insects (Mishra and Meyer-Rochow 2008) and could make investments into the visual system ineffective at high elevations.

Contrary to our expectation, there was no relationship between productivity and hind femur length of assemblages. Thus and because elevation explained only a small portion of the variability in the data, we assume that additional factors influence hind femur lengths of orthopteran assemblages. Also the pattern of eye size did not comply with our expectation of increasing eye sizes with increasing productivity, based on the high energy needed for the development and maintenance of large eyes (Prokopy 1983). Eye size decreased with increasing plant productivity. Plots with low productivity were dominated by bare ground and low vegetation cover, as indicated by the NDVI values. Open areas provide few possibilities for orthopterans to hide (e.g. between tall grasses or below bushes and trees), which makes it easier for predators to find and catch prey. Consequently, large eyes may be of particular advantage in open areas because they can enhance the early detection of predators. Even though the size of insect eyes is one of the main determinants of visual quality, the total visual performance depends also on structures independent of eye size, e.g., the architecture of the retina and the central nervous system (Land 1997, Rutowski 2000). Furthermore, the ability to detect predators will also be influenced by mechanical and chemical means of predator perception, such as hairs or olfaction (Dangles et al. 2005). Protective coloration and crypsis, however, reduce the risk of being detected by predators (Steiner 1981, Eterovick et al. 1997).

Conclusion

Our study revealed that body size as well as wing length, hind femur length, and eye size corrected for covariance with body length of orthopteran assemblages decreases with increasing elevation. Body size and relative eye size also decreased with increasing productivity (measured as NDVI). Our results support the importance of temperature as one of the main drivers of interspecific body size clines. Moreover, our findings emphasize the importance of temperature also for interspecific clines of other ecologically relevant morphological traits, independent of changes in body size. Our results suggest that orthopteran assemblages have higher fecundity, dispersal ability, escape ability, and predator detection at low elevations with high temperatures, compared to assemblages at high elevations with low temperatures. Furthermore, our results do not support the resource availability hypothesis in that assemblages were characterized by species with larger body sizes and larger eyes in areas of low productivity. These habitats were predominated by low vegetation cover and few resources, which might be linked with a high risk of starvation and predation. Hence, it seems that

the absence of vegetation resources rather than their availability favors orthopteran assemblages with energetically expensive morphological traits. Our study emphasizes that morphological adaptations involve not only adaptations of body size but also independent adaptations of other morphological traits. To better understand the ecological interactions between organisms and their environment, future studies should aim to see beyond patterns of body size and include changes of other morphological traits along environmental gradients.

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Chapter 4

Ants as indicators of environmental change and ecosystem processes

with
Jan Schlautmann | David A. Donoso | Christine I.B. Wallis | Jörg Bendix | Roland Brandl | Nina Farwig |

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Summary

Environmental stressors and changes in land use have led to rapid and dramatic species losses. As such, we need effective monitoring programs that alert us not only to biodiversity losses, but also to functional changes in species assemblages and associated ecosystem processes. Ants are important components of terrestrial food webs and a key group in food web interactions and numerous ecosystem processes. Their sensitive and rapid response to environmental changes suggests that they are a suitable indicator group for the monitoring of abiotic, biotic, and functional changes. We tested the suitability of the incidence (i.e. the sum of all species occurrences at 30 baits), species richness, and functional richness of ants as indicators of ecological responses to environmental change, forest degradation, and of the ecosystem process predation on herbivorous arthropods. We sampled data along an elevational gradient (1,000–3,000 m a.s.l.) and across seasons (wetter and drier period) in a montane rainforest in southern Ecuador. The incidence of ants declined with increasing elevation but did not change with forest degradation. Ant incidence was higher during the drier season. Species richness was highly correlated with incidence and showed comparable results. Functional richness also declined with increasing elevation and did not change with forest degradation. However, a null-model comparison revealed that the functional richness pattern did not differ from a pattern expected for ant assemblages with randomly distributed sets of traits across species. Predation on artificial caterpillars decreased along the elevational gradient; the pattern was not driven by elevation itself, but by ant incidence (or interchangeable by ant richness), which positively affected predation. In spite of lower ant incidence (or ant richness), predation was higher during the wetter season and did not change with forest degradation and ant functional richness. We used path analysis to disentangle the causal relationships of the environmental factors temperature (with elevation as a proxy), season, and habitat degradation with the incidence and functional richness of ants, and their consequences for predation. Our results would suggest that the forecasted global warming might support more active and species-rich ant assemblages, which in turn would mediate increased predation on herbivorous arthropods. However, this prediction should be made with reservation, as it assumes that the dispersal of ants keeps pace with the climatic changes as well as a one-dimensional relationship between ants and predation within a food-web that comprises species interactions of much higher complexity. Our results also suggested that degraded forests in our study area might provide suitable habitat for epigaeic, ground-dwelling ant assemblages that do not differ in incidence, species richness, functional richness, composition, or predation on arthropods from assemblages of primary forests. Most importantly, our results suggest that the occurrence and activity of ants are important drivers of ecosystem processes and that changes in the incidence and richness of ants can be used as effective indicators of responses to temperature changes and of predation within mega-diverse forest ecosystem.

Introduction

Biodiversity provides the basic elements for species interactions within food webs and ecosystem processes and is therefore a key factor for the stability of ecosystems (Chapin III et al. 1997, Cardinale et al. 2012, Tilman et al. 2012). However, rapid anthropogenic environmental and land-use changes increasingly modify the structure and extent of natural ecosystems, which can lead to a dramatic loss of biodiversity (Foley et al. 2005, Walther 2010). As such, we urgently require a continuous monitoring of the status of biodiversity and ecosystems (Scholes et al. 2008) that not only focuses on the presence or absence of certain (keystone) species, but monitors functional changes in species assemblages and their effects on food webs and ecosystem processes (Noss 1999, Palmer and Febria 2012).

Predation is an important process within food webs; predators can act at different trophic levels (De Ruiter et al. 1995) and can modify species abundances (Holt 1977), composition of assemblages (Pace et al. 1999), and evolution of traits (Peacor and Werner 2001). Ants are one of the most important generalist predators of arthropods in terrestrial ecosystems, particularly in the tropics (Hölldobler and Wilson 1990, Seifert et al. 2016). They are crucial for numerous ecosystem processes, e.g., soil turnover, nutrient cycling, plant defense, seed dispersal, and regulation of herbivores, which has led to them being widely accepted as keystone taxa (Underwood and Fisher 2006 and references within, Parr et al. 2016). Furthermore, their simple and cost-efficient sampling (Andersen and Majer 2004,

Underwood and Fisher 2006) makes them a suitable indicator of even subtle abiotic, biotic, and functional changes of ecosystems (Folgarait 1998).

The monitoring of responses to various environmental changes requires measures that match the habitat and degradation type in question (Read and Andersen 2000, Dale and Beyeler 2001, Carignan and Villard 2002, Ricotta et al. 2015, Siddig et al. 2016). Different measures of ant diversity have been successfully used to indicate ecological responses to natural abiotic changes within local habitats, such as temperature, humidity, soil, and vegetation type (Hoffmann 2010). For ants, species richness alone usually provides rather limited information on ecosystem changes, whereas data on ant abundance, species composition, and richness of functional traits (functional richness) better reflect the biotic response of the entire ecosystem (Folgarait 1998, Hoffmann and Andersen 2003, Yates et al. 2014). Many ant species are stenothermic, and thus temperature is often the main determinant of abundance, species richness, and composition of ant assemblages, with generally decreasing ant abundances and species richness with decreasing temperature (Kaspari et al. 2003, Sanders et al. 2003, 2007, Jenkins et al. 2011, Longino et al. 2014). Therefore, the projected global warming might lead to shifts in the latitudinal or elevational distribution of species as well as to an overall loss of species (Hughes 2000, Colwell et al. 2008, Gibb et al. 2015a), with consequences for ant-mediated food web interactions and ecosystem processes (Del Toro et al. 2015). In addition, seasonality influences ant assemblages; high amounts of rainfall can decrease the size of colonies and activity of ants, thereby influencing the composition of assemblages (Andersen 1986, Delsinne et al. 2013).

Beyond abiotic changes, anthropogenic habitat degradation also alters richness and composition of ant assemblages mediated through changes in habitat characteristics (Underwood and Fisher 2006, Hoffmann 2010). In general, a decrease in the complexity of habitats (e.g., the amount or characteristics of leaf litter) leads to changes in species composition (Wiescher et al. 2012, Gibb and Parr 2013, Gibb et al. 2015b). Thereby, the effect of habitat degradation on ants depends on its type and severity. In complex habitats, such as forests, fragmentation or selective logging does not necessarily affect the abundance or species richness of ants (Donoso, this special issue; Underwood and Fisher, 2006 and references within; Woodcock et al., 2011). However, secondary forest patches of differing ages in Brazil contain ant assemblages with fewer species and lower functional diversity compared to old-growth forests (Bihn et al. 2008, 2010). Furthermore, forest degradation is expected to affect the composition of ant assemblages when it is associated with changes in habitat structure, e.g., canopy openness, vegetation structure, and plant richness (Underwood and Fisher 2006, Yusah and Foster 2016). In New Guinea, higher density, larger size, and higher taxonomic diversity of trees explains more than 50% of the observed higher ant species richness of primary forests compared to secondary forests (Klimes et al. 2012).

The multitude of species responses to environmental change depend on the functional traits of species, as traits are related to habitat preference, diet, and foraging strategy (Wiescher et al. 2012, Gibb and Parr 2013, Gibb et al. 2015b). For example, the overall body size of epigaeic ant assemblages is linked to habitat complexity and trophic level (Gibb and Parr 2013), where larger ants forage at the surface rather than in the litter (Weiser and Kaspari 2006, Donoso and Ramón 2009). Epigaeic predatory ants also have larger bodies than omnivorous species (Gibb et al., 2015b), and head and mandible size are linked to prey size (Davidson 1977, Fowler et al. 1991, Kaspari 1996) and leg length is linked to foraging speed (Bartholomew et al. 1988). Given these close relationships of functional traits with habitat conditions and trophic position, it is thought that functional richness of ants is more directly linked with food web interactions and ecosystem processes than species identity *per se* (Mouchet et al. 2010). However, it is important to note that the strength of an assemblage-wide contribution to ecosystem processes will be determined not only by the number of species and their functional richness but also by the number and activity of individuals (Stuart-Smith et al. 2013).

Abiotic conditions and species traits jointly affect the composition of predator and prey assemblages, which in turn affects predation (Lavorel and Garnier 2002, Hooper et al. 2005, Lebrija-Trejos et al. 2010, Yates et al. 2014). By controlling herbivorous arthropods, predators can positively influence plant growth and regeneration (Snyder et al. 2006) and might promote persistence and stability within assemblages (Chapin III et al. 1997). Overall, rates of predation

on herbivorous arthropods decline with increasing elevation, whereby the relative contribution of the various predators might change (Hodkinson, 2005; Sam et al., 2015a). However, estimating predation rates along environmental gradients is difficult at ecosystem levels (Parr et al. 2016). To overcome these difficulties, artificial caterpillars have been used in several studies as a simple but effective method to quantify and qualify the predation on herbivorous arthropods. For instance, ants were the most important predators of artificial caterpillars in lowland rainforests of Papua New Guinea, whereas birds were the dominant predators above 1,700 m a.s.l. (Sam et al., 2015a). In addition, the predation pressure on herbivorous arthropods is influenced by seasonal rainfall, with higher attack rates on artificial caterpillars during the wetter season, which is congruent with peaks in real caterpillar density and suggests shifts in the foraging behavior or a timed phenology of the predators (Molleman et al. 2016).

Here we compared the suitability of incidence, species richness, and functional richness of epigaeic ants as indicators of responses to environmental changes and of ecosystem processes, using a simple space-for-time approach (Pickett 1989, Blois et al. 2013), nutrient baits, and artificial caterpillars. We used elevation as a proxy for temperature changes and accounted also for the effect of wetter and drier seasons and forest degradation. We investigated the relationship between environmental variables and variables characterizing ant assemblages and their functions in food webs. For the latter, we used attack marks of ants on artificial caterpillars as a measure of predation rates. We expected a decline in the incidence and species richness of ants with increasing elevation and that functional richness is a better indicator of predation and forest degradation than the incidence or richness of ants. We used a path model to disentangle the causal relationships of temperature (with elevation as a proxy), season, and habitat degradation with the incidence respectively species richness and functional richness of ants and their consequences for predation.

Methods

Study area

We conducted our study within and around the Podocarpus National Park (4°17'0''S 79°0'0''W) and the *Reserva Biológica* San Francisco (3°58'30''S 79°4'25''W) on the eastern Cordillera of the Andes in the provinces of Loja and Zamora-Chinchipe, southern Ecuador. Within the protected areas, the study area is characterized by natural primary forest. Outside of the protected lands, the forest has been mostly converted to active or inert pastures for cattle grazing (Curatola Fernández et al. 2015). This landscape is interspersed with patches of degraded secondary forest. The climate of the study area is perhumid, with a main rainy season occurring from June to August and drier month from October to January (Rollenbeck and Bendix 2011). Annual rainfall is high throughout the year, with approximately 2,000 mm at 1,000 m a.s.l. (Zamora), 2,200 mm at 2,000 m a.s.l. (ECSF-Met. Station), and 4,800 mm at 3000 m a.s.l. (Cerro Met. Station; Bendix et al., 2008a, 2008b). The mean annual air temperature decreases with elevation from 20.0 °C at 1,000 m a.s.l., to 15.5 °C at 2000 m a.s.l., to 9.5 °C at 3,000 m a.s.l. (Bendix et al. 2008a).

Study design

We established 27 study plots along an elevational gradient from 1,000 to 3,000 m a.s.l. The plots were located in natural primary forest and in secondary forest fragments at elevational levels of 1,000, 1,500, 2,000, 2,500, and 3,000 m a.s.l. with three replicates per level and type. At the highest elevational level (3,000 m a.s.l.), no forests were degraded, leading to a total of 15 plots in primary forests, and 12 plots in degraded forests. The plots reflected the typical type of natural or degraded forests at the respective elevation level. The natural forest plots comprised evergreen premontane rain forest (~ 1000 m a.s.l.), evergreen lower montane rain forest (~ 2000m a.s.l.), and evergreen upper montane rain forest (~ 3000 m a.s.l.). Outside the protected area, but within the same valley, the degraded plots comprised secondary forest fragments adjacent to active cattle pastures with varying degrees of recent and past reforestations. The degraded forest plots were embedded in a matrix of pastures and bracken-infested areas, interspersed with secondary forest fragments on inaccessible areas, e.g. at steep slopes or crags. The study plots were 1,000 m² in size (10 m x 100 m and 20 m x 50 m, depending on the landform configuration), and mean pair-wise geographic distances between

study plots ranged from 117 m to 24 km (mean ± SD: 12 km ± 8.4 km). Each study plot was subdivided into 5 subplots of 20 m × 10 m (200 m^2).

Sampling of ants and data processing

We sampled ant assemblages during two periods in 2014 (wetter season: April to August; drier season: October, November) following the baiting methods described in Peters et al. (2014). Baiting is an effective technique for recording the occurrence of ant species, especially in habitats with high litter depth (Andersen 1997). As demands for macronutrients vary and often depend on the trophic position of species, we used six different types of macronutrients to sample ant assemblages. We placed six baits with different nutrients randomly on the ground of each of the five subplots (minimum distance between each set of baits: 5–7 m) during times of high ant activity (late morning to early afternoon). The baits consisted of 50 mL plastic tubes with 15 mL of one of the following six solutions: H_2O (tap water; control); NaCl (20 g NaCl/1 L H_2O); amino acid (200 g glutamine/1 L H_20); $(CH_2O)_n$ (200 g sucrose/1 L H_2O); $(CH_2O)_n$-amino acid mix [(100 g sucrose + 100 g glutamine)/1 L H_2O]; and lipids (olive oil). As ant activity and walking speed positively correlate with temperature (Hurlbert et al. 2008, Jayatilaka et al. 2011), the timespan between setting the bait and attracting the highest number of ant species is shorter in environments with higher ambient temperatures than in cooler areas (Vogt et al. 2003). To determine the respective best-suited timespan at each elevational level, we observed the accumulation of ants on nutrient baits for extended periods. This timespan for plots at 1,000, 1,500, 2,000, 2,500, and 3,000 m a.s.l. was 2, 3, 4, 4.5, and 5 h, respectively. At these time points, we collected the respective baits and all ants within or at the opening of the bait tube.

All ants were identified to the morpho-species or species level. The ant fauna of Ecuador consists of at least 650 species, but it is taxonomically poorly defined (Salazar et al. 2015). Therefore, we established a mitochondrial cytochrome *c* oxidase I (COI) barcode reference library to refine our definition of morpho-species (see also Domínguez et al., 2016). COI barcodes for the ant species were obtained in collaboration with the Biodiversity Institute of Ontario using sequencing techniques and tools in the Barcode of Life Database (BOLD; Ratnasingham and Hebert, 2007). New sequences for the study were uploaded onto the BOLD database (www.boldsystems.org/) and are available under DOI: dx.doi.org/10.5883/DS-SANFRAF, with GenBank accession numbers KY441904 to KY442061. We compared our specimens with those deposited at the Ecuadorian Ant Reference Collection (ARCE), housed in Instituto de Ciencias Biológicas of the Escuela Politécnica Nacional, and curated by D. A. Donoso. Ants identified to morpho-species bear an ARCE morpho-species number. Voucher specimens of all species and morpho-species have been deposited in the ARCE collection and the Museum at Universidad Técnica Particular de Loja.

The relative use of the nutrient baits filled with NaCl, $(CH_2O)_n$, $(CH_2O)_n$-amino acid, and lipids decreased with increasing elevation (all effect sizes negative, $p < 0.001$), whereas amino acid baits and water control baits did not show a significant pattern ($p > 0.05$). Likewise, the morphological trait constitution of ant species was not related to the used nutrient types. As differences in nutrient preferences do not affect our subsequent analyses, we will in the following report the summary statistics of ant assemblages captured across all bait types. We used the total number of species in all 30 bait tubes as a measure of species richness within the plots during the two seasons. Several ant species demonstrate recruitment behavior to monopolize nutrient sources; this can lead to decreasing ant species richness or an overestimation of numbers of individuals after the arrival of a dominant species at a bait (Davidson 1998). We therefore calculated the incidence of ants (instead of abundances based on sums of individuals) as the sum of the number of occurrences of each species at all baits. For example, the occurrence of one species at three baits, another species at five baits, and a further species at one bait would result in an incidence value of nine, independent of the number of individuals or the total number of occupied baits. Ant incidence therefore is a mixed measure of the occurrence, species richness, and (foraging) activity of the ant assemblage. We consequently expect a high correlation between the incidence and richness of ants. Additionally, we used a null model to test for deviations of the observed incidence-elevation relationship from a pattern expected with a random distribution of ant incidences across the elevational gradient. Differences between observed patterns and random patterns from null models indicate that eco-

logical processes structured the observed pattern; such ecological processes include filtering from the environment (observed values are lower than null-model values; underdispersion) and competition (observed values are higher than null-model values; overdispersion). For the null model, we shuffled the incidence values of the species-incidence matrix 1,000 times, while maintaining the frequencies of species incidences (fixed column sums) with the function randomizeMatrix from the add-on package picante (Kembel et al. 2010) in R (R Core Team 2017). This null model leads to ant assemblages with random incidences across the elevational gradient. Afterwards, we calculated standardized effect sizes for the incidence of ants as ses$X$ = $[X_{\text{observed}} - \text{mean}(X_{\text{random}})]/\text{sd}(X_{\text{random}})$, where X_{observed} is the observed incidence of ants, mean (X_{random}) is the mean of the randomizations of the null-model, and sd (X_{random}) is the standard deviation of the randomly calculated ant incidence.

To analyze changes in the composition of species along the elevational gradient and with forest degradation, we conducted a detrended correspondence analysis for the combined dataset of ant incidence across both seasons. Detrended correspondence analysis eliminates the arch effect of correspondence analyses by detrending. For example, the first axis is divided into segments in which the samples are centered to have a mean of zero for the second axis, and a similar process was used for higher axes. Compression of the ends of the gradients was corrected by nonlinear rescaling, in which sample scores were shifted along each axis by an average width of one (Hill and Gauch 1980). This procedure leads to axes that are scaled in units of species standard deviation and resembles beta diversity. We used the function decorana and fitted elevation and forest degradation onto the ordination using the function envfit with 999 permutations. Both functions are implemented in the add-on package vegan (Oksanen et al. 2016).

Calculation of functional richness of ant assemblages

To calculate the functional richness of ant assemblages, we used continuous measures of four morphological traits that are related to predatory behavior (Yates et al., 2014 and references within): Weber's length (a proxy for the overall size), head length (indicative of diet), mandible length (longer mandibles allow larger prey), and length of the hind femur (linked to foraging speed). We measured these traits on 1–5 individuals per species depending on the number of individuals available and calculated the mean value per species. We could not obtain trait measures for the mandible length of 11 ant species because mandibles of the specimen were not intact or measurements were not possible; this constituted 12% of the total number of ant incidences: genus *Camponotus* (1 species), *Myrmelachista* (2 species), *Nylanderia* (1 species), *Pheidole* (2 species), and *Solenopsis* (5 species). For these species, we used the mean trait value of the genus. Furthermore, we excluded the species *Pseudomyrmex termitarius* (contributing altogether five incidences on two plots) from the calculation of functional richness as we could not obtain trait data for the species, and it was the only representative of its genus. To achieve normal distribution, we $\log_{10}$-transformed all trait variables before statistical analysis. Furthermore, we corrected for covariance of body part measures and overall body size (Stern and Emlen 1999) by using residuals of linear regressions against the Weber's length as response variables (Kaspari and Weiser 1999, Gibb and Parr 2013). Pearson product-moment correlation coefficients (PPMC) between the four morphological ant traits Weber's length, head length, mandible length, and hind femur length were always < 0.40. We calculated the (raw) functional richness (FRic) of ant assemblages as a measure of the volume of a convex hull around all species of an assemblage projected onto a multidimensional trait space using principal coordinates analysis (PCoA) based on the Euclidean distances between species traits (Villéger et al. 2008) and the function dbFD from the add-on package FD (Laliberté and Legendre 2010) in R (R Core Team 2017). We standardized FRic by dividing the FRic values by the maximum possible FRic value of a fictitious ant assemblage consisting of all recorded ant species. The standardized FRic values could therefore range between 0 (plot without any ant species) and 1 (plot with all possible species). We achieved similar results when we used a Hutchinsonian hypervolume approach to calculated functional richness (Blonder et al., 2014). For simplicity, we will not report the results of the hypervolume approach. To test whether the raw FRic values differed from values expected under a random trait distribution, we calculated the standardized effect sizes of FRic (ses FRic) using the same approach as for the incidence of ants, by randomizing the

rows of the species-traits matrix 1,000 times, while keeping the trait combinations fixed (random trait combinations are biologically not meaningful).

Predation rate on artificial caterpillars

To quantify predation rates (attacks by natural enemies) on herbivorous arthropods, we used 300 artificial caterpillars within each study plot. We exposed the artificial caterpillars on 30 randomly selected plants in the shrub layer (0.5 to 2.0 m above ground; low damage by herbivores) of each plot by pinning 10 artificial caterpillars with a thin wire onto the surface of 10 leaves of each plant. Artificial caterpillars consisted of green-colored (to mimic palatable and undefended prey; see Howe et al., 2009), oil-based, and non-toxic plasticine (STAEDTLER® Noris Club 8421). We pressed the plasticine through a syringe to ensure comparable shape and thickness (20 mm long and 2–3 mm in diameter), as well as a smooth surface. After five days, we recollected all artificial caterpillars; 467 (2.9%) of the exposed artificial caterpillars fell to the ground or could not be recovered and were excluded from the analysis. All recovered artificial caterpillars were directly inspected for bite marks, which were assigned to predator groups (ants, bees and wasps, birds, others) using the bite-mark catalogue of Low et al. (2014). If bite marks were not directly identifiable, we examined them more carefully in the lab using a magnifying lens. As we could not differentiate bite marks from one or more predation events and made by one or several predator individuals, we assessed predation qualitatively instead of quantitatively, i.e., predated/not predated. As ants were by far the most abundant predators of artificial caterpillars across the studied gradient (> 70%), we only used ant predation events in our analyses and calculated predation as the percentage of artificial caterpillars with bite marks made by ants.

Path analyses

We conducted two separate path models for ant incidence and richness due to high multicollinearity between both measures ($r^2 = 0.9$; PPMC; Tu et al., 2005). Due to the nested structure of our data and because of the binomial distribution of the predation data, we tested the path models after Shipley's directional separation method (Shipley 2009) within the R environment (R Core Team 2017). We conducted the confirmatory path analysis using three mixed effect regressions to test the initially assumed direct and indirect effects of abiotic factors (elevation as proxy for temperature, season, and degradation) on ant incidence (respectively species richness), ant functional richness, and predation of artificial caterpillars by ants. To account for the nested structure of our data (sampling of wetter and drier season nested in plot), we included study plot as a random effect in all models to correct for pseudo replication. To allow for comparison of the path model coefficients of the fixed effects, we z-transformed all predictor variables in the three regressions and the response variables from regression one and two. These first two regressions included the effects of elevation, season, and forest degradation on the incidence of ant species (respectively species richness) and raw functional richness. To account for the potential relationship between the incidence of ants (respectively species richness) and functional richness, we included species incidence in the second regression. To test the conditional independence of nested data, we used linear mixed effect models with normal error distribution (LMER; function lmer in the add-on package lme4; Bates et al., 2015) and fitted the LMERs using restricted maximum-likelihood estimation (REML). The third regression included the effects of elevation, season, forest degradation, ant incidence (respectively species richness), and ant functional richness on the predation of artificial caterpillars. In addition, we included a random factor for each observation event to remove overdispersion (Harrison 2014). In this case, we used a generalized linear mixed effect model

Table 1. Distribution of ant individuals, incidence (a combined measure of ant occurrence and activity; for details, see Methods section), and species richness during the wetter season and drier season and on natural plots and degraded plots.

Season	Plot type	Individuals	Ant incidence	Species richness
Wetter season	Natural	1,002	137	44
	Degraded	1,034	141	46
Drier season	Natural	1,610	208	51
	Degraded	1,264	205	52

with binomial error distribution (GLMER; function glmer in the add-on package lme4; Bates et al., 2015) and fitted the model using a maximum-likelihood estimation (Laplace approximation). We derived the P-values from z-tests of estimated model coefficients using the function cftest from the add-on package multcomp (Hothorn et al. 2008). We applied d-separation to test each hypothesized conditional independency separately using the LMERs and GLMER to obtain the probability that the partial slope of the dependent variable was significantly different from zero. We combined and tested the probabilities of all independence claims using *C* statistics (Shipley 2009).

In a next step, we compared the performance of both path models (ant incidence and richness) by performing bootstrap analysis of regression models two (functional richness) and three (predation). To do so, we ran these two regressions of both path models based on 1000 bootstrap samples of the original data. Then, we compared the AIC values of the bootstrap regressions between the path model of ant incidence and richness using t-statistics. This comparison revealed no significant differences between the performance of regressions of incidence and species richness (all $p > 0.9$; Welch's t-test). To facilitate the readability, we will in the following report the results using ant incidence only, but emphasize that they apply equally for species richness. We included results of the model of species richness in the Supplementary material.

Results

Ant incidence

In total, we recorded 4,910 ant individuals across the 27 study plots. The sum of ant incidences at all baits was 691; the number of species at the same bait ranged from 0 to 4. We used ant incidence as a combined measure of the overall richness, occurrence, and (foraging) activity of ant species on the plots; we defined ant incidence as

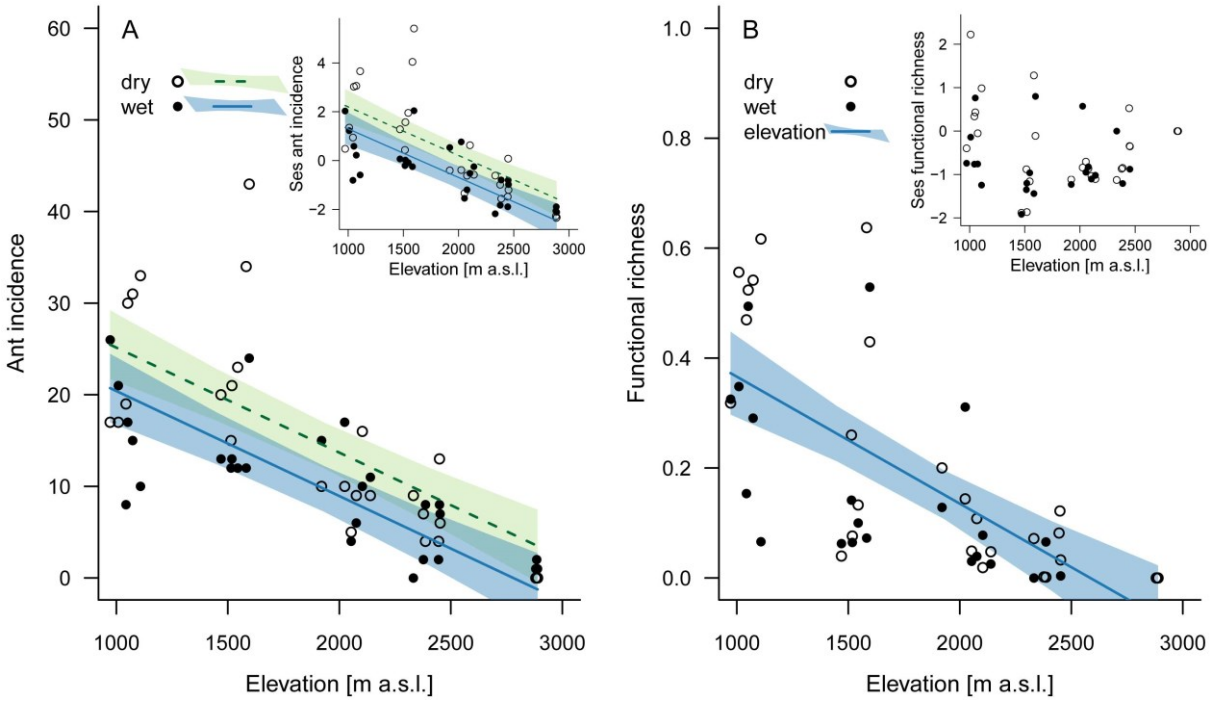

Figure 1. A) Loss in ant incidence (a combined measure of ant occurrence and activity, i.e., occurrence of ant species across 30 baits; for details, see Methods section), and loss in standardized effect size of ant incidence (ses ant incidence; inset), and B) loss in functional richness, and loss in standardized effect size of functional richness (ses functional richness; inset) with increasing elevation in the study area. Functional richness was based on four morphological traits. Standardized effect sizes are based on 1000 randomizations of the rows of the species-incidence and species-traits matrix; for details, see Methods section). Shown are the effects of (A) season and (B) elevation from linear mixed-effects models and 95% confidence intervals. Open circles, underlying raw data for ant incidence and ses ant incidence (A) and functional richness and ses functional richness (B) in the drier season; filled circles, that in the wetter season.

Table 2. Changes in ant incidence (a combined measure of ant occurrence and activity, for details, see Methods section; model 1), (raw) functional richness of ant assemblages (model 2), and predation of artificial caterpillars (model 3) with elevation, drier vs. wetter season, and forest degradation. Linear mixed effect models were used for models 1, and 2, and a generalized linear mixed effect model was used for model 3. Study plots were included as random effect in models 1–3 to correct for pseudoreplication; model 3 included each observation as a random effect to remove overdispersion. Boldface indicates significant values. Results equally apply for species richness, see Supplementary Table 4.1 in Appendix.

Source of variation	Estimate	*z-value*	*p-value*
Model 1: Ant incidence			
Elevation	$-7.2 * 10^{-1}$	−7.2	< **0.001**
Season	$2.5 * 10^{-1}$	2.9	< **0.01**
Degradation	$-7.1 * 10^{-3}$	−0.071	0.94
Model 2: Functional richness			
Elevation	$-3.2* 10^{-1}$	0.14	**0.017**
Season	$8.9* 10^{-2}$	0.96	0.34
Degradation	$-4.7* 10^{-2}$	−0.53	0.34
Ant incidence	$5.8* 10^{-1}$	4.6	< **0.001**
Model 3: Predation of artificial caterpillars			
Elevation	$-8.5* 10^{-2}$	−0.41	0.69
Season	$-5.3* 10^{-1}$	−3.7	< **0.001**
Degradation	$1.1* 10^{-1}$	0.87	0.38
Ant incidence	$6.2* 10^{-1}$	2.7	< **0.01**
Functional richness	$2.2* 10^{-2}$	0.099	0.92

the sum of all species occurrences across 30 baits. Ant incidence was highly correlated with species richness ($r^2 = 0.90$, $p < 0.001$; PPMC). The sampled individuals belonged to 87 ant species, which could be divided into 9 species and 78 morpho-species, from 5 subfamilies (Dolichoderinae, Formicinae, Myrmicinae, Ponerinae, and Pseudomyrmicinae) and 14 genera. The number of ant individuals, incidences, and species differed between seasons, but the number in natural forests was similar to that in degraded forests (Table 1). The observed ant incidence and also the standardized effect size of ant incidence decreased with elevation (Table 2; Fig. 1 A). Ant incidence was higher in the drier season than in the wetter season, and forest degradation had no significant effect (Table 2; Figs. 1A and 2). Species richness showed a pattern similar to ant incidence (Supplementary Table 4.1 in Appendix). The first decorana axis was strongly and positively correlated with elevation ($r^2 = 0.92$, $p < 0.001$; PPMC), but not with degradation ($r^2 = 0.0089$, $p = 0.72$; PPMC; for decorana visualization, see Supplementary Figure 4.1 in Appendix).

Functional richness

The functional richness calculated from the four ant morphological traits (Weber's length, head length, mandible length, and hind femur length) ranged from 0.0 to 0.64 (0.18 ± 0.20; mean ± SD). The (raw) functional richness decreased with elevation and was most strongly and positively affected by ant incidence (Table 2; Figs. 1 B and 2) and species richness (Supplementary Table 4.1 in Appendix). Neither forest degradation nor season influenced the functional richness of the sampled ant assemblage (Table 2). Yet, the relationship between functional richness and elevation became insignificant when using standardized effect sizes instead of raw values, which indicated that the pattern of the (raw) functional richness does not differ from a pattern expected for ant assemblages with randomly distributed

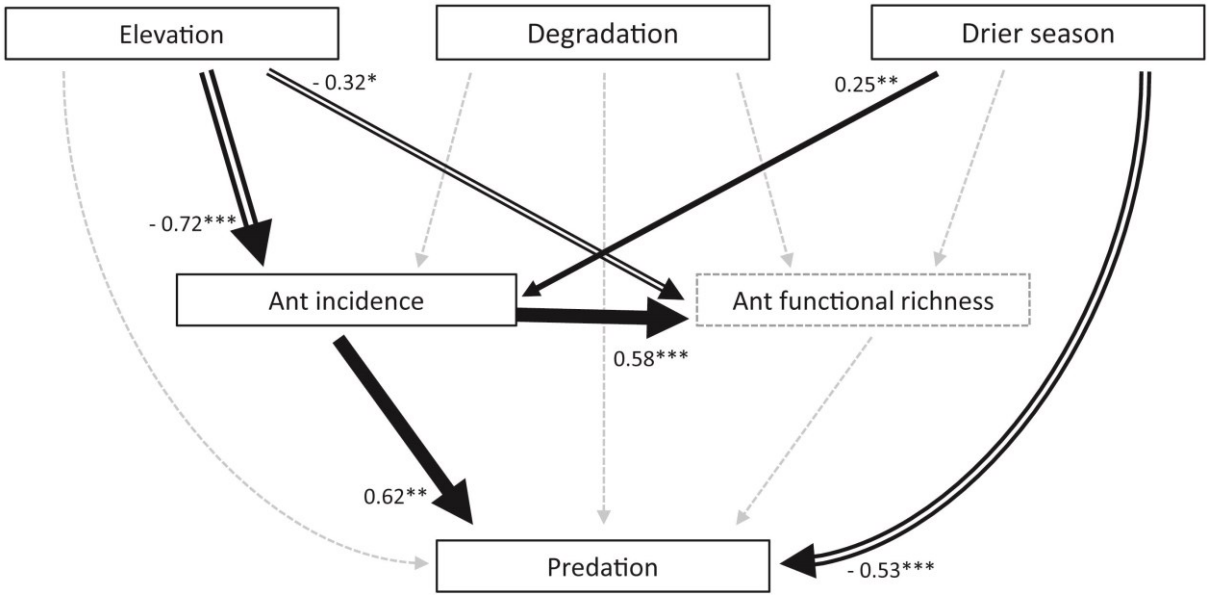

Figure 2. Path model of relationships between elevation (as proxy for changes in temperature), season, forest degradation, ant incidence (a combined measure of ant occurrence and activity, i.e., occurrence of ant species across 30 baits; for details, see Methods section), functional richness of ants, and predation of artificial caterpillars. The thickness of the solid arrows depict the values of the estimated effect sizes next to arrows; values in black and solid arrows indicate significant positive effects, framed arrows indicate significant negative effects with asterisks demarking the significance level (0.050 < * > 0.010 < ** > 0.001 < *** > 0.000; ant incidence is a combined measure of ant occurrence and activity; for details, see Methods section). Note that ant functional richness does not differ for ant assemblages with randomly distributed sets of traits across species (indicated by dashed frame; cf. Figure 1B; for details, see Methods and Results section). Results equally apply for species richness, see Supplementary Figure 4.2 in Appendix.

sets of traits across species (Fig. 1 B).

Predation rate

In total, we identified 2,119 bite marks on 15,733 collected artificial caterpillars. Most of the bite marks originated from ants (1,540 marks; 73 %), followed by wasps and bees (201 marks; 9.5 %), birds (133 marks; 6.3 %), and unknown predators (245 marks; 12 %). The predation rate of ants on artificial caterpillars across 5 days ranged from 0.0 to 0.36 (0.099 ± 0.081; mean ± SD). In general, predation rates decreased with increasing elevation (estimate elevation = −4.9*10−5, p = 0.0057, r^2 = 0.14), but the effect of elevation on the predation rate of artificial caterpillars was caused by ant incidence (Table 2; Fig. 2). Ant incidence and species richness affected predation rate on artificial caterpillars positively, whereas drier season had a direct negative effect on the predation rate, but an additional indirect positive effect caused by ant incidence (Table 2; Fig. 2). Forest degradation neither influenced any aspect of ant assemblages nor the predation of artificial caterpillars (Table 2). Replacing ant incidence by species richness within the same path model yielded similar patterns of the main pathways (Supplementary Figure 4.2 in Appendix). The result of the Chi²-test for independence supported the assumptions of both path models (path model with ant incidence: X^2 = 6.3; df = 12; P-value = 0.90; path model with species richness: X^2 = 5.9; df= 12; P-value = 0.92).

Discussion

Ant incidence was highly correlated with species richness without significant differences in reaction to abiotic factors and as predictors of functional richness and predation. Incidence and richness of ants declined with elevation and increasing rainfall (wetter vs. drier season), whereas forest degradation did not affect both measures. Functional richness was mainly driven by the incidence (respectively richness) of ants. The predation rate on artificial caterpillars decreased along the elevational gradient. Most importantly, ant incidence (respectively richness) and season directly affected the predation rate on artificial caterpillars, whereas elevation and raw functional richness did not have direct effects on

the predation rates.

Ants as indicators of responses to environmental changes

We quantified ant incidences, i.e., a measure of the occurrence and (foraging) activity of ants, by using an easily implementable approach based on baits with six different nutrient types. The observed ant incidence (as well as the standardized effect sizes) and richness clearly decreased along the elevational gradient, which was even more pronounced as the time of exposure of the baits was increased with increasing elevation. Furthermore, the community composition of ants markedly changed with elevation, which indicated a high species turnover along the elevational gradient (Longino et al. 2014, Bishop et al. 2014, Nowrouzi et al. 2016). Temperature is one of the most important abiotic predictors of the decline in ant species with elevation as it limits the activity of ants and thus the access to resources (Sanders et al., 2007; but also see Kaspari et al., 2000). Season was an abiotic factor that also influenced the incidence and species richness of ants, with higher ant incidence during the drier season. This typical finding (Basu, 1997; El Keroumi et al., 2012; but also see Castro et al., 2012) might be attributed to higher foraging activity at higher temperatures (Medeiros et al. 2014), seasonal changes in the brood cycle, or availability of nest sites or food (Levings 1983). However, in our study, higher ant activity did not seem to translate into higher predation in the herbal and shrub layers, but might be instead limited to ground-foraging activity (see subsection 4.3). The main driver of the raw functional richness was the incidence of ants. As ant incidence was highly correlated with species richness ($r^2 = 0.90$, $p < 0.001$) and species-rich assemblages are likely to comprise more diverse functional traits, habitats with high ant incidence will also have higher functional richness (Cadotte et al. 2011). The raw functional richness of ant assemblages also decreased with elevation, which we confirmed by using a Hutchinsonian hypervolume approach (data not shown; Blonder et al., 2014). Reymond et al. (2013), who found a similar pattern in the Swiss National Park, explained this finding with the filtering effect of the environment in which only species with traits adapted to harsh environmental conditions at high elevations can tolerate the habitat (also see, e.g., Machac et al., 2011). However, our finding of no elevation pattern for the standardized effect sizes indicates that the raw functional richness is mainly driven by declining ant incidence respectively richness and is not actually a filtering effect of the environment; this suggests that the measured functional traits are independent from elevation.

When we consider ants as indicators of responses to environmental changes, it should be stressed that the effects of global warming are already noticeable in the study area. Meteorological stations within and near the study area have evidenced a significant warming of at least 0.6 °C within the last 45 years of 1961–2008 (Bendix et al. 2010, Peters et al. 2013), and future projections of the Intergovernmental Panel on Climate Change (IPCC) point to a further warming of the study area of around +4 °C by 2100, with the assumption that greenhouse gas concentrations will be high in 2100 (936 ppm CO_2 and high radiative forcing of 8.5 W/m²; RCP8.5scenario; Meinshausen et al., 2011). A temperature increase of +4 °C by 2100 at the actual average lapse rate in the study area of −0.52 °C per 100 m (Bendix et al., 2008) would predict an elevational shift of the pattern of ant incidence and richness of approximately 80 m per decade. Based on the results reported here and assuming a one-dimensional relationship between temperature and species richness, we would expect an approximately 1.3- to 4-fold increase in species richness by 2080 (from 38 to 51 species at 1,500 m a.s.l., from 23 to 38 species at 2,000 m a.s.l., from 12 to 23 species at 2,500 m a.s.l., and from 3 to 12 species at 3,000 m a.s.l.). However, interrelationships among changes in temperature, seasonal patterns of precipitation, and species interactions are complex and difficult to predict. Our finding of opposing effects of drier season on ants and the predation process supports this assumption. In addition, predictions of changes in species distributions based on changes in abiotic conditions usually do not consider, e.g., whether the ability of a species to disperse will keep pace with the increasing temperature or how competition between species will influence species composition (Chapin III et al. 2000). Therefore, projections can be made only with reservations (Colwell et al. 2008, Lavergne et al. 2010).

Ants as indicators of forest degradation

In contrast to findings of several other studies (e.g., Philpott et al., 2010 and references within;

for a review see Underwood and Fisher, 2006), forest degradation in our study area did not have an effect on the incidence, richness, and raw functional richness of ant assemblages, or on assemblage composition. Habitat degradation mainly affects ant assemblages through changes in local factors, such as abiotic changes in soil and microclimatic conditions, including moisture, temperature, and exposure (Philpott et al. 2010). Our results match findings of Donoso et al. (this issue), who report no change in litter ant community composition after 15 years of continuous monitoring in a secondary cloud forest in northern Ecuador. Furthermore, low impact land use, such as traditional crop and pasture systems may sometimes lead to an increase of ant abundances (Folgarait 1998). However, other analyses indicate that the composition of traits, functional groups, or occurrence of specialized ants might change, even if numbers of ants do not change (Hoffmann and Andersen 2003, Leal et al. 2012, Peters et al. 2014a, Fotso Kuate et al. 2015). Two reasons may explain our results: On the one hand, our findings suggest that the present forest degradation of the abiotic and biotic conditions in our study area might not be severe enough to negatively affect the ground-foraging ant assemblages in degraded forests or that the ant assemblages managed to recover: Ant assemblages are able to reach levels of species richness and species compositions similar to that of natural forests after several decades of even acute degradation events in the past (Ryder Wilkie et al., 2009; but also see Bihn et al., 2008). Also, a high connectivity of the matrix habitat that connects the degraded and natural forests in our study area may have contributed to similar ant assemblages in degraded and natural forest plots (Harrison and Bruna 1999, Hunter 2002, Schoereder et al. 2004). Moreover, all degraded forest plots were in close proximity to forest edges. Edge effects might have induced an increase of the depth and quality of the leaf litter (compared to the interior of degraded forests), making the litter more similar to the litter in natural forests (Philpott et al. 2010). However, we cannot finally determine the principal reason for the absence of a degradation effect on the epigaeic ant assemblages, as we do not have data on the degradation history, age, matrix connectivity, and litter quality of the degraded forest plots. On the other hand, our baiting method used might also have contributed to our results. It is thought that nutrient baits mostly attract generalist ant species. As specialized ant species are assumed to react more strongly to changes in habitat quality, we might have missed the more sensitive portion of the ant assemblage. Additionally, our baiting approach collected ants from ground-dwelling assemblages and canopy-dwelling ants may react differently and more strongly towards degradation (Yanoviak and Kaspari 2000, Floren et al. 2002, Klimes et al. 2015).

Ants as indicators of predation

We quantified predation based on ant bite marks on artificial caterpillars that can be easily integrated in the practice of ecosystem management. Even though attack rates on artificial caterpillars of different materials might differ (Sam et al. 2015b), an increasing number of studies use model caterpillars as surrogates for predation rates on real caterpillars (Low et al., 2015; Meyer et al., 2015 and references within). Almost three-quarters (73%) of the observed attack marks in our study originated from ants, which supports the importance of ants as a major group of predators of herbivorous arthropods in rainforests (Seifert et al. 2016). Predation of artificial caterpillars decreased with increasing elevation, which reflects the pattern of ant incidence and richness and supports the findings of Sam et al. (2015a). Surprisingly, the predation of artificial caterpillars was significantly higher in the wetter season than in the drier season, which contrasts the pattern of higher ant incidence (respectively richness) during the drier season. This finding could be explained by the positive relationship between resource availability and foraging activity of ants (Medeiros et al., 2014; but also see Raimundo et al., 2009). For instance, a peak of predation rates on artificial caterpillars during the wetter season has also been found in submontane forests in Uganda (Molleman et al. 2016). The authors explained the predation maximum with the simultaneous peak in prey density, which would lead to responses of the foraging or breeding activity of the predators. However, Brehm (2002) found no marked seasonal changes of moth communities in our study area. Lower predation of artificial caterpillars during the drier season but a simultaneously high incidence of ants would therefore suggest a shift of the ants foraging activity from the foliage layer to more abundant resources, e.g., in the leaf litter, but further studies are needed to test this assumption.

Elevation, forest degradation, or the raw functional richness of ants did not explain the variation in predation of artificial caterpillars. We expected that the functional richness of ant assemblages was related to predatory behavior; therefore, we in turn expected that ant functional richness would be more strongly related to predation rates than the overall incidence or species richness of ants. Yet, the functional traits measured (Weber's length, and length of head, mandible, and hind femur) might not be ecologically linked to the rate of predation events. Alternatively, as we used only one type of artificial caterpillar, which did not move or emit visual or chemical cues used by predators to locate their prey, possibly only one type of predatory ant was attracted, which would also make the functional richness measure irrelevant. However, predation experiments comparing attack rates on live and artificial caterpillars made of either dough or plasticine revealed no significant differences (Sam et al., 2015b). Nevertheless, Sam et al. (2015b) did not test whether their single type of caterpillar prey, although one of the most common species in the understory, attracted a representative portion of all possible predators of the diverse group of herbivorous arthropods. Even though we cannot completely eliminate these methodological doubts, our finding of no association between functional richness and predation underlines that the occurrence, richness, and activity of species are more important drivers of ecosystem processes than their functional measures (Stuart-Smith et al. 2013).

Conclusion

Our findings highlight the applicability of simple monitoring tools for studying ant assemblages and related predation rates. We found that incidence of ants as a measure of ant occurrence and activity, as well as species richness can be used as suitable indicators of responses to rising temperatures and of predation, but not of forest degradation within complex rainforest ecosystems. Rising temperatures might favor more abundant, species-rich, and active ant assemblages and therefore higher predation rates in montane forests at higher elevations if dispersal of ants keeps pace with the climatic changes. However, projections can only be made with reservations, as other species interactions e.g. between herbivores and plants will additionally affect the responses of the same food web, which is of much higher complexity. Our finding that forest degradation did not affect any of the studied biotic aspects proposes lightly degraded forests as suitable habitat for functional epigaeic ant assemblages. Thereby, our results suggest that the occurrence, richness, and activity of functional taxa might be more important for the functioning of related ecosystem processes than their functional measures. Our findings also suggest that the incidence and species richness of ants are suitable indicators of changes in abiotic conditions and are also functional indicators of an important ecosystem process. Hence, simple measures such as ant incidence and species richness can supersede the use of more labor-intensive, trait-based measures for quantifying the functionality of ecosystems.

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Chapter 5

Synthesis

Biodiversity provides the basis for species interactions and ecosystem functioning. However, anthropogenic impacts – habitat degradation and climate change being the most severe – lead to dramatic declines in biodiversity and have even caused researchers to warn against the Earth's sixth mass extinction (Ceballos et al. 2015). Decreasing biodiversity comprises a loss of taxonomic, genetic, and functional richness which affects ecosystems and related ecosystem processes. Despite its importance for effective conservation management, we are still far from a comprehensive understanding of the patterns of biodiversity, the processes that determine these patterns, impacts of changing environmental conditions, and the relationships between biodiversity and ecosystem functioning. Elevational gradients are well suited to study responses of species assemblages and their different taxonomic, phylogenetic, and functional components with changing environmental conditions. In this thesis, I focused on these different components of biodiversity to *i)* investigate assembly processes of tropical trees, *ii)* study responses of functionally important morphological traits of orthopteran assemblages to changes in temperature and productivity, and *iii)* disentangle relationships between changes in temperature, seasonality, and habitat degradation and the incidence, species richness, and functional richness of ants and the subsequent effects on the ecosystem process predation of herbivorous arthropods, thereby testing the suitability of ants as functional indicators for effective ecosystem monitoring.

Phylogenetic diversity – a mirror for processes behind species assembly

In the second chapter, I aimed to reveal assembly processes of tropical tree assemblages in the Andes. I studied patterns of species richness, phylogenetic diversity, and family age of tree assemblages to test predictions from the phylogenetic niche conservatism hypothesis (PNC) along an elevational gradient in the Ecuadorian Andes. Based on the latest available phylogenetic megatree of plants and age estimates for branch length calibration, I calculated two different phylogenetic diversity measures and the mean family age of tree assemblages. The two phylogenetic diversity measures focus on different evolutionary time scales of the phylogenetic structure of assemblages: The mean nearest taxon distance (MNTD) detects patterns close to the tips of the phylogenetic tree and therefore reflects the most recent evolutionary history. The mean pairwise phylogenetic distance (MPD) detects tree-wide patterns of the phylogenetic structure of co-occurring species. The mean family age resembles patterns from the deepest nodes within the phylogenetic tree.

My findings contrast predictions from the PNC, which would suggest decreasing species richness, phylogenetic diversity, and decreasing mean family ages with decreasing temperatures along the studied elevation gradient. Instead, MPD and family age of tree assemblages increased with elevation, whereas species richness and MNTD were not related to elevation. Furthermore, tree assemblages were generally phylogenetically clustered which suggests environmental filtering as the main driver of tree assembly along the studied gradient.

My results revealed that the occurrence of elements from old gymnosperm and angiosperm floras with extra-tropical origins at high elevations drive the phylogenetic and family age pattern of tree assemblages. This suggests that extra-tropical taxa with adaptations to temperate environments followed a corridor of temperate habitats that emerged in the course of the Andean uplift during the Neogene (Hoorn et al. 2010) to finally reach the high elevation habitats in the tropics (Segovia and Armesto 2015). The relatively young geographical history of the Andes, therefore, plays a major role in today's composition of tree assemblages in the Andes (Qian 2014). These findings challenge the general applicability of the PNC for tropical elevation gradients. Furthermore, the findings underline that the recent tree assemblages in the Ecuadorian Andes were shaped by an interplay of ecological processes (environmental filtering), biogeographic events (the uplift of the Andes), as well as historical processes (immigration of flora elements with extra-tropical origins). The biogeographic history of mountains can, therefore, play important roles for the composition of recent tree assemblages along elevational gradients.

Functional diversity – traits form the basis for interactions between species and their environment

In the third chapter, I aimed to reveal relationships between changing environmental factors and interspecific changes of body size and other morphological traits. In particular, I studied how four different morphological traits of orthopteran assemblages respond to changes in temperature and productivity along an elevational gradient at Mt. Kilimanjaro (Tanzania). The four traits cover four ecologically important aspects of Orthoptera assemblages: Body size is related to fecundity, wing length influences dispersal ability, hind femur length relates to jumping ability, and eye size is positively related to predator detection. First, I calculated a multivariate measure of the overall body size of species of ten morphological traits. I corrected the morphological traits for covariation with body size and used community weighted means as a measure of interspecific trait values. Finally, I used Bayesian linear mixed-effect models to analyze the effects of elevation (as a proxy for temperature) and productivity on the trait values of orthopteran assemblages.

I found that body size decreased linearly with increasing elevation. Independently of the pattern of body size, the relative wing length, hind femur length, and eye size also decreased with increasing elevation. My findings emphasize the importance of changes in temperature not only for body size but also for other morphological traits of orthopteran assemblages. The effect of temperature on body size is suggested to derive from temperature-dependent biochemical processes that shorten larval growth periods, and negatively affect growth rates (van der Have and de Jong 1996, Chown and Gaston 2010). Low temperatures at high elevations also decrease the metabolic rates of insects which hampers flight ability (Dillon et al. 2006) and would make the maintenance of long wings and flight ability resource intensive. The decrease of hind femur length and eye size might rather suggest a potentially decreasing predator pressure with increasing elevation. Besides temperature, productivity negatively affected body size and eye size of orthopteran assemblages. Productivity is positively linked to the availability of plants that provide hiding abilities and resources for orthopteran species. Areas with low productivity may, therefore, be associated with an increased risk of predation and starvation (Denno et al. 2003). Habitats with low productivity might thus favor Orthoptera assemblages with larger body sizes that reduce starvation risk, as well as larger eyes that enhance predator detection. The results underline that morphological adaptations to changing environmental conditions go beyond changes in body size and involve independent adaptations of other morphological traits. The inclusion of other morphological traits in studies of size clines along environmental gradients can, therefore, help to better understand interactions between organisms and their environment.

Functional diversity – a driver of ecosystem processes

In the fourth chapter, I aimed to test the suitability of different measures of ant assemblages as indicators of ecological responses to environmental changes, habitat degradation, and of the ecosystem process predation of herbivorous arthropods. To do so, I studied the relationships between changes in elevation (as a proxy for temperature), season, and habitat degradation on the incidence, species richness, and functional diversity of ants and their combined effects on the predation process along an elevational gradient in the Ecuadorian Andes. First, I used an easily applicable baiting approach to sample the epigaeic ant assemblages. Then I determined the incidence and species richness of the ant assemblages. I used the multidimensional trait space of four predation-related morphological traits of ants to obtain a measure of the functional richness of ant assemblages. Furthermore, I quantified the predation of herbivorous arthropods using artificial caterpillars made of plasticine. In the last step, I used a path analysis to disentangle the causal relationships between the environmental factors temperature, season, and habitat degradation and the incidence, species richness, and functional diversity of ants and their combined effect on predation rates.

Both ant incidence and species richness decreased with increasing elevation and were higher during the dry season. Ant incidence and richness positively affected the predation of artificial caterpillars. These findings suggest that the forecasted global warming would support more active and species-rich ant assemblages, which would mediate increased predation of herbivorous arthropods. Opposing the finding of ant in-

cidence and richness, predation rates were lower during the dry season and higher during the wet season. This emphasizes that relationships between changes in temperature, precipitation, species assemblages, and ecosystem processes are complex and therefore difficult to predict (Colwell et al. 2008, Lavergne et al. 2010). Surprisingly, I did not find significant effects of habitat degradation on the incidence or species richness of ants, nor on the predation of herbivorous arthropods. This suggests that degraded forests in the study area provide a suitable habitat for epigaeic, ground-dwelling ant assemblages that resemble assemblages in natural forests in terms of their incidence, richness, and predation of herbivorous arthropods. However, it is important to consider that the sampling approach (bait traps) might not have attracted resource-specialized ant species that might be more sensitive to habitat degradation. The functional richness of ant assemblages decreased with elevation, however, a null-model comparison revealed that the functional richness measure was biologically not meaningful. The measured traits were thus mainly driven by ant incidence instead of elevation. Altogether, my results suggest that the incidence and species richness of ants can serve as effective indicators of responses to changes in temperature and precipitation and of the ecosystem process predation of herbivorous arthropods.

Conclusion

The presented studies represent three different approaches of current biodiversity research. The joint consideration of the three studies illustrates the versatility of different biodiversity components, covering aspects from assembly processes (chapter 2), interactions between the environment and species traits (chapter 3), right up to relationships between environmental conditions, species, and ecosystem processes (chapter 4). As an understanding of the different components of biodiversity is an important precondition for its protection, the results of the studies can contribute to effective conservation management.

All presented studies mirror the effectiveness of elevational gradients to gain a better understanding of the mechanisms that shape the distribution of biodiversity across environmental gradients. Furthermore, they support the widely recognized impact of temperature on species assemblages. Temperature played a major role in the phylogenetic structure of tropical tree assemblages, where evolutionary old taxa with adaptations to temperate conditions drove the increase of phylodiversity with increasing elevation. Temperature also was the main determinant of size clines of morphological traits of orthopteran assemblages at Mt. Kilimanjaro. And temperature directly affected the incidence and species richness of ants and therefore indirectly affected the ecosystem process predation of herbivorous arthropods. The overall importance of temperature on the biodiversity within aquatic and terrestrial ecosystems is already widely acknowledged (Garcia et al. 2014, Yasuhara and Danovaro 2016). Temperature changes due to global climatic changes will therefore certainly affect the future composition of species assemblages, the interactions between species and their environment, as well as ecosystem processes across the globe. While changes in distribution patterns of species have already been detected (Lenoir and Svenning 2015), the current ecological knowledge is still far from being sufficiently comprehensive to allow reliable predictions of future ecosystem responses to global warming.

In the second chapter, regarding the phylogenetic pattern of recent tree assemblages in the Ecuadorian Andes, I showed that phylodiversity provides useful measures to detect assembly processes that shaped the composition of recent species assemblages. Moreover, I found a distinct pattern of decreasing mean family age of tree assemblages with increasing elevation. This pattern was less distinct for the mean pairwise phylogenetic distance, whereas the mean nearest taxon distance was not related to elevation. When aiming to gain a comprehensive understanding of assembly processes, the comparison of phylogenetic measures that focus on different evolutionary time scales is therefore promising. Moreover, future advances in the resolution and time calibration of phylogenetic mega trees will allow more precise conclusions about the processes behind temporal changes in diversity patterns (see chapter 6 – Perspectives).

Furthermore, my results revealed that expected patterns derived from the phylogenetic niche conservatism hypothesis (PNC) do not apply to the studied elevational gradient. However, PNC is often used to explain the pattern of decreasing taxonomic and phylogenetic diversity with decreasing tropicality along latitudinal gradients (Wiens et al. 2010). My contradictory find-

ings are surprising because elevational gradients are often suggested as useful representatives for environmental changes along latitudinal gradients (Graham et al. 2014). On the one hand, the nestedness of elevational gradients within biogeographic regions allows minimizing effects of large-scale environmental variation which can complicate studies along latitudinal gradients (Körner 2000, Sundqvist et al. 2013). On the other hand, the complexity due to the entanglement of ecological and historical relationships across latitudes and their differing impacts on species assemblages can complicate the transferability between elevational and latitudinal gradients (Graham et al. 2014). My findings, therefore, underline that temperature changes do not necessarily lead to similar patterns and processes along elevational and latitudinal gradients. Moreover, historic processes that can strongly impact migration corridors and therefore dispersal abilities of lineages, should not be underestimated in their possible impacts on the structure of current species assemblages.

In the third chapter, I showed that environmental conditions affect body size and independently from body size, also the wing length, hind femur length, and eye size within orthopteran assemblages. Morphological traits incorporate species identity by adding ecologically meaningful characteristics on species that were traditionally characterized only by their taxonomic name (Dehling et al. 2016). Compared to measures of phylodiversity, morphological traits, therefore, allow an understanding of direct relationships between species and environmental conditions. Despite their importance for the fitness of species, interspecific changes of morphological traits other than body size are still highly underrepresented in studies of size clines along environmental gradients. A shift of the current research towards an integration of other ecologically important morphological traits can, therefore, benefit our understanding of the composition of species assemblages as a result of changing environmental conditions (Violle et al. 2007).

In the fourth chapter, I showed that the incidence and species richness of ants can be used as effective indicators of climatic changes and of the ecosystem process predation of herbivorous arthropods. Furthermore, my study revealed that the integration of relatively complex trait measures, such as functional diversity, do not necessarily contribute to a better understanding of ecosystem processes. In spite of experimental evidence of relationships between certain traits and ecosystem processes, trait related measures do not need to reflect the actual complexity of the ecological system and the functioning of ecosystem processes by default (Mlambo 2014). There are several possible options that can lead to not meaningful trait-based measures. First, the measured traits are functionally unimportant or are not involved in the process under consideration (I will further discuss this aspect in the Perspectives Section in chapter 6). Second, ecological factors other than functional diversity may be more important for the respective ecosystem process and third, functional diversity has no effect (Petchey and Gaston 2006). Furthermore, methodical coherences can additionally complicate the use of trait-based measures. The generation of averaged assemblage values from trait values of co-occurring species can lead to internal statistical relationships of no biological significance and required corrections are still not common (Zelený and Schaffers 2012, Hawkins et al. 2017). This can lead to measures of functional diversity that are mainly driven by the abundance or richness of species (Poos et al. 2009), which I also revealed in my study. These possibilities demonstrate that an inconsiderate use of trait-based measures could lead to a pseudo-complexity without ecological meaning, emphasizing the importance of experimental tests of functional traits on ecosystem processes (Mlambo 2014). Yet, correctly applied measures of functional traits and functional diversity may yield novel insights that go beyond insights from taxonomic approaches.

In the context of practical conservation and its management, taxonomic approaches might be better suited than functional approaches for the monitoring of ecosystems and ecosystem processes. On the one hand, functional diversity measures require a relatively high effort and time which makes them costlier than species-based approaches. Furthermore, in case of positive correlations with functional diversity, simple taxonomic diversity measures can indirectly be indicative of ecosystem functioning (Petchey and Gaston 2002, Funk et al. 2017). On the other hand, it is also possible that ecosystem processes depend less on the overall functional diversity within assemblages and rather change with the quality or quantity of organisms (Frainer et al. 2014, Schleuning et al. 2015). For example, if trait quality is important, the occurrence of only one

key species could be sufficient to sustain the functioning of an ecosystem process, while the functional diversity of such a one species-assemblage would be extremely low (Winfree et al. 2015; but also see Mouillot et al. 2013, Valiente-Banuet et al. 2015). The occurrence of key species that have a large influence on a certain process is more likely in assemblages with high taxonomic diversity, which could also explain the often observed positive effect of taxonomic diversity on ecosystem functioning. However, relationships between the importance of species identity and diversity and ecosystem processes can be context dependent. A meta-analysis that focused on primary productivity, nutrient uptake, herbivory, and decomposition found for example, that single highly productive species can, in most cases, outperform diverse polycultures (Cardinale et al. 2011). Whereas another recent study found that synergistic species interactions (diversity) rather than the influence of a few important species drive the growth of tree stems (Grossman et al. 2017). Apart from the quality, also the quantity or abundance of individuals can be important for the functioning of an ecosystem process. Assemblages with low taxonomic and functional diversity, but with high abundances of individuals may contribute more to an ecosystem process than assemblages with high taxonomic and functional diversity and low abundances of individuals (Winfree et al. 2015). I could show that ant incidence, a mixed measure of the occurrence and activity of ant species, performed equally well as a predictor of the predation of herbivorous arthropods as species richness. Furthermore, another recent study found that the pollination of watermelon and blueberry was driven by fluctuations in the abundance of common bee species, regardless of species richness and composition (Genung et al. 2017). These findings underline the importance of the presence and activity of individuals as the fundamental basis for any interaction within ecosystems. Accordingly, a loss of the number of ecological interactions may affect the functionality of ecosystems at a faster rate than the disappearance of species (Valiente-Banuet et al. 2015). Simple measures such as the abundance of individuals or species should therefore not be underestimated in their ecological significance (Winfree et al. 2015, Soliveres et al. 2016), as well as in their versatility as monitoring tools within conservation programs.

Altogether, the results of my thesis show how the different components of biodiversity research can contribute to a better understanding of the distribution of biodiversity and the functioning of ecosystems, which provides the foundation for effective conservation management. Progressing impacts from anthropogenic land use and climate change will continue to profoundly affect species assemblages across the globe. The intensity and peculiarity of anthropogenic changes are thereby unique in the history of the planet and caused researchers to declare the beginning of a new geological epoch – the Anthropocene (Waters et al. 2016). To better understand the past, recent, and future processes that shape the global biodiversity, studies that focus on measures of phylogenetic diversity, functional traits, and functional diversity are therefore still vital. Furthermore, these measures can also help to foresee potential effects of environmental changes on biodiversity and the consequences for ecosystem functioning. However, the rapid degradation of natural ecosystems also requires effective monitoring of the status of ecosystems (Palmer and Febria 2012). For this purpose, relatively simple measures that base on the activity, abundance or taxonomic diversity of species assemblages will remain of prime importance in the future. Their significance, as well as their relative cost efficiency and simplicity compared to the more complex phylogenetic and functional measures, makes them promising for a broad application in management practice. The development of a wide range of simple as well as sophisticated approaches and measures is therefore essential for the future of biodiversity research and conservation.

Chapter 6

Perspectives

Biodiversity research currently experiences a period of prosperity and, at the same time, faces an overall bias in the geographical coverage of studies. While tropical regions are of essential importance for the conservation of global biodiversity (Myers et al. 2000), most studies on diversity patterns and ecosystem processes are done in Europe (Seppelt et al. 2011, Verheyen et al. 2016, Clarke et al. 2017). The evolutionary history of ecosystems, the interactions between traits and environmental conditions, and the influence of traits on ecosystem processes are highly context-dependent (Hooper et al. 2005). Therefore, generalizations for biodiversity patterns, especially such of phylogenetic and functional diversity, require more studies from tropical ecosystems (Clarke et al. 2017).

In the present thesis, I found tropical tree assemblages to be generally phylogenetically clustered, suggesting environmental filtering as an important driver of community assembly. The effect of abiotic filters on species is one of the most studied aspects of biodiversity research, and the overall importance of environmental conditions on the structure of species assemblages is beyond dispute. However, studies that use observational data to draw conclusions on environmental filtering are currently under consideration. Only recently, the concept of environmental filtering has been criticized and is being questioned as the sole driver of clustered assemblage structures (Kraft et al. 2015, Cadotte and Tucker 2017). Environmental filtering is expected to lead to phylogenetically and functionally clustered assemblages because the species that cannot resist the prevailing abiotic conditions should – under the assumption of phylogenetically conserved traits – be phylogenetically and functionally similar (Emerson and Gillespie 2008). However, apart from abiotic factors, also biotic factors, such as the absence of pollinators or the presence of certain predators, can act as a filter of similar taxa from assemblages (Kraft et al. 2015). Moreover, phylogenetically or functionally similar species could co-occur at a site if they require only minimal niche differences to stabilize their coexistence and if they have a higher intrinsic growth rate than other species. In this case, competition between similar co-occurring species would also lead to a clustered assemblage structure (Cadotte and Tucker 2017). Patterns of phylogenetic or functional clustering alone would thus be insufficient to draw conclusions on the presence of environmental filtering as the only structuring process. Consequently, it cannot be ruled out that conclusions from observational data that suggest environmental filtering as a structuring process are actually the result of biotic factors, local competition or a combined effect of abiotic and biotic filtering and competition (Cadotte and Tucker 2017). To truly reveal whether a species passes through an environmental filter or not, experimental tests of species survival in the absence of other species are vital (Kraft et al. 2015). Following Kraft et al. (2015), several steps are necessary to distinguish environmental filtering from related phenomena: *i)* To distinguish environmental filtering from dispersal limitation, it is important to verify that a species has the potential to arrive at the site, for example via direct quantification of the arrival of seeds, the proximity to potential source populations, and estimates of dispersal distances. *ii)* Assess the ability of the species to tolerate the abiotic conditions present at the site in the absence of biotic interactions. For this step, it would be needed to remove or exclude all interacting species in an experimental setup or to test physiological tolerances of species in a laboratory context. Interactions that are not removed would consequently be lumped into the effect of abiotic conditions. *iii)* Assess the ability of the species to persist at the site in the presence of neighbors, for example through experimental invasions. Furthermore, it is important to test for positive interactions with other species (facilitation) that increase the fitness of species or may allow species to tolerate otherwise unsuitable conditions. It is obvious that this approach involves high logistical challenges and will make it difficult to put it into practice across complex ecosystems. However, ascribing patterns of clustering as evidence for environmental filtering can otherwise lead to overestimation of the role of the abiotic environment and may depreciate the influence of biotic interactions in shaping species assemblages (Kraft et al. 2015). Even though the central role of abiotic factors on the distribution of biodiversity is not in doubt, experimental approaches could sharpen our understanding of assembly processes.

Ecological studies that use phylogenies to reveal assemblage structures are all based on the assumption that the used phylogeny correctly represents evolutionary history (Rangel et al. 2015). One of the key issues for phylogenetic studies of tropical assemblages is therefore the low resolution of phylogenies of tropical species.

The extraordinarily high number of tropical species tremendously increases the effort needed for fully resolved phylogenies of tropical taxa. However, the resolution of phylogenetic trees, e.g. the portion of resolved phylogenetic nodes across the phylogenetic tree, or polytomies at genus levels, can impact the results of studies on phylogenetic assemblage structures (Kress et al. 2009, 2010, Davies et al. 2012). Advances in the phylogenetic resolution of the evolutionary relationships between tropical species will thus require reviews of the results from studies that used less well-resolved phylogenies. This will reveal whether the current knowledge of phylogenetic relationships allowed researchers to draw the right conclusions. However, there are also new future possibilities for phylogenetic studies, as more precise phylogenetic data on ages of families as well as on relationships between genera and species will provide opportunities to reveal the more recent processes that structure assemblages (Lamsdell et al. 2017). Patterns of mean ages that focus on the recent evolution of species, e.g. mean genus age or mean species age, could show completely different patterns compared to mean family ages. It would be highly interesting to link more recent speciation events within assemblages to past changes in climate, environmental conditions, and extreme events (Violle et al. 2014). Moreover, the phylogenetic structure of assemblages never is at an equilibrium state and it will be another future challenge to follow the imminent changes in the taxonomic and phylogenetic composition of assemblages and to reveal the structuring forces of the Anthropocene (Gerhold et al. 2015). Future research could therefore enable a more precise definition of the possibilities and limitations of evolution which could contribute to better predictions of future reactions of whole assemblages to environmental changes and would help to direct conservation efforts towards the most vulnerable ecosystems (Mouquet et al. 2012).

The understanding of relationships between species and their traits to environmental conditions and for ecosystem functioning is still in its beginning. One of the most pressing challenges, therefore, is to experimentally test relationships between taxonomic diversity, traits, the functionality of species and of assemblages, and their effects on ecosystem processes. As discussed earlier, this could address the limitation of trait-based studies that most often rely on the assumption that the measured traits correctly represent functional information (Cadotte et al. 2013, Mlambo 2014). Improving collaborative data sharing as well as a standardized trait methodology across taxa can thereby be one important step to push our current knowledge forward (Moretti et al. 2017). In this context, it will be especially relevant that a balanced share of the studies is located in tropical ecosystems. The difference in the amount of taxonomic diversity within temperate and tropical ecosystems makes it unclear if results from biodiversity-ecosystem functioning research can be extrapolated across climatic zones. The higher taxonomic diversity in tropical ecosystems could lead to a higher resilience of ecosystem processes – a loss of single species would in turn only weakly affect the functioning. Contrastingly, the higher ecological specialization of tropical species could also lead to stronger effects of a loss of a single species on ecosystem functioning (Clarke et al. 2017). As the current theories on ecosystem functioning have mainly been developed in temperate ecosystems, they may not apply to the tropics. Extending research on biodiversity and ecosystem functioning into more complex tropical ecosystems is, therefore, a crucial task for the future (Clarke et al. 2017).

Finally, ecosystems provide the basis for multiple functionally important processes. These processes are likely to be partially influenced by the same species, which can lead to trade-offs as well as synergies between multiple ecosystem processes and functions (Zavaleta et al. 2010). This suggests that the functioning of an increasing number of ecosystem processes requires an increasing number of species. In turn, studies on single processes may underestimate the level of biodiversity that is required to maintain multifunctional ecosystems (Hector and Bagchi 2007). Nevertheless, research on multifunctionality of ecosystem processes is still in its early stages. Future studies should, therefore, seek to characterize traits across taxonomic groups and trophic levels, as well as their interrelationships across large spatial scales and their direct and indirect effects on multiple ecosystem processes (Lavorel et al. 2013). Two types of studies can contribute to this newly emerging field of research: *i)* Studies within ecosystems that differ in biodiversity and ecosystem functioning. The measured ecosystem functions, e.g. biomass production, predation, and herbivory could be correlated to the taxonomic, phylogenetic or functional diversity of trees, predators, and herbivores (Nock et al.

2017). On the one hand, such monitoring approaches reflect natural conditions of ecosystems and are therefore of particular realism and relevance. On the other hand, correlations between several explanatory variables can make it impossible to separate single effects on ecosystem multifunctionality, making them less useful for the detection of causal relationships among variables. *ii)* Studies that use a balanced experimental design and synthetic gradients of biodiversity, while keeping environmental conditions constant, for example by using microcosms (Slade et al. 2017). These experimental approaches allow to analyze the effects of two or more explanatory variables independently and can reveal causal relationships among variables. However, the lack of actual complexity within real ecosystems can make it difficult to translate the results to field conditions (Nock et al. 2017) and the logistic effort of multi-taxa approaches can be enormous. Moreover, the influence of environmental conditions on ecosystem processes, as for example revealed in chapter 4 of this thesis, is likely to make relationships between biodiversity and multifunctionality more complex (Perkins et al. 2015, Salas-Lopez et al. 2017). A comprehensive understanding of the functioning of ecosystems, therefore, requires further studies (both observational and experimental approaches) that focus on groups from multiple trophic levels as well as on several ecosystem processes under consideration of changing environmental conditions.

Meeting these challenges will contribute to the profound knowledge that is needed to enable competent conservation management of ecosystems which provide us with important ecosystem functions. Last but not least, it will therefore be a further challenge for the future to ensure that the scientific insights from biodiversity research will find their way into applied conservation.

Chapter 7

Deutsche Zusammenfassung

Biodiversität umfasst die Vielfalt innerhalb von Arten, zwischen Arten und von Ökosystemen. Sie stellt somit eine wichtige Grundlage für Interaktionen zwischen Arten, für Ökosystemprozesse und Ökosystemfunktionen dar. Anthropogene Einflüsse, z.B. Landnutzungsänderungen und Klimawandel, führen weltweit zu Veränderungen und Verlusten der Biodiversität, die sich wiederum auf die Stabilität und Funktionalität der Ökosysteme auswirken. Um Biodiversität und funktionelle Ökosysteme langfristig und effektiv erhalten und schützen zu können, ist ein umfassendes Verständnis von Biodiversität und ihrer taxonomischen, phylogenetischen und funktionellen Komponenten wichtig. Dazu gehört sowohl *i)* ein Verständnis der Verteilung von Biodiversität, als auch der Prozesse, die zu dieser Verteilung beitragen. Darüber hinaus bedarf es fundierten Wissens über *ii)* die Einflüsse von sich ändernden Umweltbedingungen auf Artengemeinschaften und *iii)* ein Verständnis der Beziehung zwischen den Biodiversitätskomponenten und Ökosystemprozessen. Entlang zweier tropischer Höhengradienten habe ich Muster der taxonomischen, phylogenetischen und funktionellen Komponenten von Biodiversität genutzt, um zu einem besseren Verständnis dieser drei Aspekte beizutragen.

In einer Studie in den ecuadorianischen Anden habe ich mich mit der Zusammensetzung tropischer Baumartengemeinschaften und der sie beeinflussenden ökologischen und historischen Prozesse beschäftigt. Im Rahmen dieser Studie konnte ich zeigen, dass sich die Anzahl der Baumarten entlang des untersuchten Höhengradienten (~ 1000 – 3000 m ü. NN) nicht veränderte. Im Allgemeinen war die Vielfalt der evolutiven Abstammungslinien (Phylodiversität) auf den Untersuchungsflächen geringer als auf Grund des Artenpools zu erwarten wäre. Dieses Ergebnis legt nahe, dass Umweltvariablen (sogenannte Filter) das Vorkommen von Baumarten bestimmter Linien verhindern. Darüber hinaus konnte ich zeigen, dass sowohl die Phylodiversität, als auch das durchschnittliche evolutive Familienalter der vorkommenden Baumarten entlang des Höhengradienten zunahm. Dieses Muster wurde durch das Vorkommen von Baumarten aus den Gruppen der Angiospermen (Bedecktsamer) und Gymnospermen (Nacktsamer) getrieben. Diese gehörten überdurchschnittlich alten Pflanzenfamilien an, die ihren Ursprung in temperaten, nicht-tropischen Gebieten haben. Diese Ergebnisse legen nahe, dass einige Vertreter dieser Linien mit Anpassungen an temperates Klima einem Ausbreitungskorridor temperater Bedingungen folgten, der sich im Rahmen der Entstehung der Andenkette im Zeitalter des Paläogen (~ 65 bis ~ 23 mya) und Neogen (~ 23 mya bis 2,6 mya) bildete. Insgesamt zeigt diese Studie, dass sowohl ökologische (Umweltfilter), biogeographische (Hebung der Anden) und historische (Ausbreitung) Prozesse starken Einfluss auf die Zusammensetzung der heutigen Baumartengesellschaften in den tropischen Bergregenwäldern haben.

In einer weiteren Studie habe ich mich den Zusammenhänge zwischen Umweltbedingungen und morphologischen Merkmalen von Artengemeinschaften gewidmet. Morphologische Merkmale haben erheblichen Einfluss auf die Fitness von Arten, da sie direkt die Wirkungen von Umweltbedingungen auf Organismen beeinflussen. Entlang eines Höhengradienten (~ 700 – 4400 m ü. NN) am Kilimandscharo in Tansania habe ich Zusammenhänge zwischen Temperatur und Habitatproduktivität und der Körpergröße, Flügellänge, Länge des hinteren Oberschenkels und Augengröße von Heuschreckengemeinschaften (Orthoptera) untersucht. Die drei letzteren Merkmale habe ich für Kovarianz mit Körpergröße korrigiert. Die mittlere Körpergröße, sowie die mittlere Flügellänge, Oberschenkellänge und Augengröße der Heuschrecken nahm konsistent mit abnehmender Temperatur entlang des Höhengradienten ab. Dieses Ergebnis verdeutlicht die Rolle von Temperatur als einen wichtigen Einflussfaktor auf die Körpergröße und andere morphologische Merkmale von Organismen. Bei wechselwarmen Organismen wirken sich abnehmende Temperaturen im Allgemeinen negativ auf temperaturabhängige biochemische Prozesse aus und führen beispielsweise zu geringeren Wachstumsraten und Verkürzungen von Wachstumsperioden im Larvenstadium. Außerdem ist die Stoffwechselrate bei niedrigen Temperaturen gering, so dass das Aufrechterhalten energieintensiver Merkmale, wie z.B. Flugmuskulatur und lange Flügel mit hohem Energieaufwand verbunden wäre. Die Verkürzung des hinteren Oberschenkels und die Verkleinerung der Augen mit zunehmender Höhe deuten auf einen abnehmenden Prädationsdruck hin, da diese Merkmale die Erkennung von Prädatoren und Fluchtmöglichkeiten positiv beeinflussen. Darüber hinaus zeigen meine Ergebnisse eine Abnahme der Körper- und Augengröße von Heuschreckengemeinschaften mit zu-

nehmender Habitatproduktivität. Habitatproduktivität ist mit der Verfügbarkeit von pflanzlicher Nahrung und Versteckmöglichkeiten unter Vegetation verknüpft. Größere Körpergrößen können daher in Gebieten mit knapper Nahrung vorteilhaft sein, denn auf Grund größerer Energiereserven verringern große Körper das Risiko zu verhungern. Große Augen wiederum verbessern das Erkennen von Prädatoren, was in Gebieten mit wenig Deckung vorteilhaft sein kann. Diese Studie zeigt anschaulich, dass die Einbeziehung morphologischer Eigenschaften helfen kann, unser Verständnis der Beziehungen zwischen Umweltbedingungen und Artgemeinschaften zu verbessern.

In einer dritten Studie habe ich wieder entlang eines Höhengradienten (~ 1000 – 3000 m ü. NN) der ecuadorianischen Anden gearbeitet, um die Beziehungen zwischen Umweltbedingungen, Ameisengemeinschaften und deren Einflüsse auf den Ökosystemprozess Prädation pflanzenfressender (herbivorer) Insekten zu untersuchen. Dabei habe ich mittels eines Pfadmodells die Effekte von Temperatur, Regen- bzw. Trockenzeit und Habitat-Degradation in fragmentierten Sekundärwäldern auf das Vorkommen von Ameisenarten bzw. den Artenreichtum von Ameisen, und die funktionelle Diversität von Ameisen untersucht. Das Modell enthielt des Weiteren die Effekte dieser Faktoren auf die Prädationsrate herbivorer Insekten (gemessen als Prädationsrate an Knetraupen). Auch diese Studie zeigt einen starken Einfluss von Temperatur: Sowohl das Vorkommen von Ameisenarten als auch deren Artenzahl nahm mit fallender Temperatur entlang des Höhengradienten ab und beide Maße waren während der Trockenzeit höher als in der Regenzeit. Das Vorkommen von Ameisenarten bzw. die Artenvielfalt der Ameisen war positiv mit der Prädationsrate der Knetraupen korreliert. Die beiden Maße der Ameisengemeinschaften könnten somit als Indikatoren für den Prädationsprozess dienen. Darüber hinaus macht diese Studie deutlich, dass Temperaturänderungen indirekt beispielsweise über Änderungen der Aktivität oder Häufigkeit von Arten ebenfalls Ökosystemprozesse beeinflussen können. Im Gegensatz zum Einfluss auf die Ameisengemeinschaften, war die Prädationsrate während der Trockenzeit geringer als während der Regenzeit. Dieses Ergebnis gibt einen Hinweis auf die tatsächliche Komplexität der Beziehungen zwischen Umweltbedingungen, Artengemeinschaften und Ökosystemprozessen. Ob beispielsweise eine Erhöhung der Temperatur durch den globalen Klimawandel tatsächlich zu einer Erhöhung der Prädationsrate im untersuchten Gebiet führen würde, ist schwer zu sagen, da viele weitere Faktoren die Zusammenhänge beeinflussen. Habitat-Degradation hatte weder auf die untersuchten Ameisengemeinschaften, noch auf den Prädationsprozess einen signifikanten Einfluss. Dieses Ergebnis deutet darauf hin, dass fragmentierte Sekundärwälder einen wichtigen Beitrag zur Erhaltung von Ameisengemeinschaften leisten können. Die Gemeinschaften in Sekundärwäldern scheinen denen in Primärwäldern in Bezug auf Aktivität, Artenreichtum und Beitrag zum Prädationsprozess vergleichbar zu sein. Allerdings könnte die angewandte Methode der Ameisenerfassung (Köderfallen) dazu geführt haben, dass spezialisierte Ameisenarten, die empfindlicher auf Habitat-Degradation reagieren, nicht erfasst wurden.

Meine drei Studien zeigen deutlich die Vielseitigkeit verschiedener Aspekte der Biodiversitätsforschung, die uns Einblicke *i)* in die Prozesse hinter der Zusammensetzung von Artengemeinschaften, *ii)* in Interaktionen zwischen Umweltbedingungen und den morphologischen Eigenschaften von Arten, und *iii)* in die Zusammenhänge zwischen Umweltbedingungen, Arten und Ökosystemprozessen geben kann. Meine Studien veranschaulichen beispielhaft die Nützlichkeit von Höhengradienten als natürliche Forschungslabore und bestätigen den starken Einfluss von Temperatur auf Biodiversität und Ökosystemprozesse. Alle Studien demonstrieren außerdem die hohe Komplexität der Beziehungen zwischen Umweltbedingungen, Arten und Ökosystemprozessen. Nichts desto trotz wird in der dritten Studie deutlich, dass auch einfache Aktivitätsmaße, in diesem Falle von Ameisengemeinschaften , als Indikatoren für komplexe Ökosystemprozesse (hier die Prädation von herbivoren Insekten) dienen können. Das Verstehen von komplexen Zusammenhängen zwischen Biodiversität und dem Funktionieren wichtiger Prozesse innerhalb von Ökosystemen ist eine wichtige Grundvoraussetzung für deren effektiven Schutz. In einem Zeitalter zunehmender Beeinflussung von Ökosystemen durch den Menschen kann die Übertragung und Anwendung der Erkenntnisse aus der Biodiversitätsforschung daher einen wichtigen Beitrag zum Erhalt gesunder und widerstandsfähiger Ökosysteme leisten.

Chapter 8

Appendix chapter 2

Phylogenetic niche conservatism does not explain elevational pattens of species richness, phylodiversity and family age of tree assemblages in Andean rainforest

Supplementary Table 2.1

Locations of the study plots.

Study site	Elevational range [m a.s.l.]	Geographic position	Area
Bombuscaro	1020 to 1268	S 04°07', W 78°58’	Podocarpus National Park
San Francisco	1913 to 2089	S 3°58', W 79°4'	Reserva San Francisco
Cajanuma	2789 to 2900	S 04°07', W 79°11'	Podocarpus National Park

Supplementary Methods 2.1

Newick version of the megatree (R20120829mod.new, Markus Gastauer, personal communication), which was used for the construction of the tree phylogeny.

((((ophioglossaceae)ophioglossales, (psilotaceae)psilotales)ophioglossaceae_to_psilotaceae, ((equisetaceae)equisetales, (marattiaceae)marattiales, ((osmundaceae)osmundales, ((hymenophyllaceae)hymenophyllales, (gleicheniaceae, (dipteridaceae, matoniaceae)) gleicheniales, ((lygodiaceae, (anemiaceae, schizaeaceae)) schizaeales, ((marsileaceae, salviniaceae)salviniales, ((thyrsopteridaceae, ((loxomataceae, (culcitaceae, plagiogyriaceae)) , (cibotiaceae, cyatheaceae, dicksoniaceae, metaxyaceae)))cyatheales, (lindsaeaceae, saccolomataceae, (dennstaedtiaceae, pteridaceae, ((aspleniaceae, woodsiaceae, thelypteridaceae, (blechnaceae, onocleaceae)) aspleniaceae_to_onocleaceae), (dryopteridaceae, (lomariopsidaceae, (tectariaceae, (oleandraceae, (davalliaceae, polypodiaceae))))) drypteridaceae_to_polypodiaceae)dennstaedtiaceae_to_polypodiaceae)polypodiales)cyatheales_to_polypodiales)marsileaceae_to_polypodiales)lygopodiaceae_to_polypodiales)hymenophyllaceae_to_polypodiales)osmundales_to_polypodiales)equisetales_to_polypodiales)monilophyte, (((cycadaceae, zamiaceae)cycadales, (ginkgoaceae, ((pinaceae, ((araucariaceae, (podocarpaceae, phyllocladaceae)) araucariaceae_to_podocarpaceae, ((cupressaceae, taxaceae)taxaceae_to_cupressaceae, sciadopityaceae)))pinales, (gnetum, ephedra, welwitschia)gnetales)gnetales_to_pinales)ginkgoaceae_to_gnetales)gymnosperms, ((amborellaceae)amborellales, ((hydatellaceae, (cabombaceae, nymphaeaceae)) nymphaeales, ((austrobaileyaceae, (trimeniaceae, schisandraceae)) austrobaileyales, (((chloranthaceae)chloranthales, (((myristicaceae, (magnoliaceae, ((degeneriaceae, himantandraceae), (annonaceae, eupomatiaceae)))) magnoliales, (calycanthaceae, ((siparunaceae, (gomortegaceae, atherospermataceae)) , (monimiaceae, (hernandiaceae, lauraceae)))) laurales), ((canellaceae, winteraceae)canellales, ((hydnoraceae, lactoridaceae, aristolochiaceae), (piperaceae, saururaceae)) piperales)) magnoliids), ((((((((((commelinaceae, hanguanaceae), (philydraceae, (haemodoraceae, pontederiaceae))) commelinales, (musaceae, heliconiaceae, (strelitziaceae, lowiaceae)strelitziaceae_to_lowiaceae, ((marantaceae, cannaceae), (zingiberaceae, costaceae))) zingiberales), ((typhaceae, bromeliaceae), (rapateaceae, (((xyridaceae, eriocaulaceae), (mayacaceae, (thurniaceae, (cyperaceae, juncaceae)cyperaceae_to_juncaceae))), ((anarthriaceae, (centrolepidaceae, restionaceae)), (flagellariaceae, ((joinvilleaceae, ecdeiocoleaceae), ((anomochloa, streptochaeta), (pharus, ((guaduella, puelia), ((((streptogyna, (ehrharta, (oryza, leersia))), ((pseudosasa, chusquea), (buergersiochloa, ((lithachne, olyra), (eremitis, pariana))))), (brachyelytrum, ((lygeum, nardus), ((melica, glyceria), (((diarrhena, (brachypodium, (avena, (bromus, triticum)))), ((phaenosperma, anisopogon), (ampelodesmos, (piptatherum, (stipa, nassella)))))))))) bep, (micraira, (((chasmanthium, (thysanolaena, zeugites)), (gynerium, (danthoniopsis, ((miscanthus, zea), (panicum, pennisetum))))), (eriachne, (((aristida, stipagrostis), (merxmuelleraa, (danthonia, (karoochloa, austrodanthonia)))), (((molinia, phragmites), (amphiopogon, arundo)), ((merxmuellerab, centropodia), ((pappophorum, (eragrostis, uniola)), (distichlis, (zoysia, (spartina, sporobolus))))))))))pacc))))poaceae)poaceae_to_flagellariaceae)))))poales, (arecaceae)arecales, dasypogonaceae)commelinids, (orchidaceae, ((boryaceae, (blandfordiaceae, (lanariaceae, (asteliaceae, hypoxidaceae)))))), ((ixioliriaceae, tecophilaeaceae), (doryanthaceae, (iridaceae, (xeronemataceae, (xanthorrhoeaceae, (amaryllidaceae, asparagaceae)))))))asparagales), ((corsiaceae, campynemataceae), ((melanthiaceae, (petermanniaceae, (colchicaceae, alstroemeriaceae))), ((rhipogonaceae, philesiaceae), (smilacaceae, liliaceae))))liliales), ((velloziaceae, triuridaceae, (stemonaceae, (pandanaceae, cyclanthaceae)))pandanales, (nartheciaceae, (burmanniaceae, dioscoreaceae))dioscoreales)), (petrosaviaceae)petrosaviales)petrosaviidae, (araceae, (tofieldiaceae, (((hydrocharitaceae, butomaceae), alismataceae), (scheuchzeriaceae, (aponogetonaceae, (juncaginaceae, ((posidoniaceae, (ruppiaceae, cymodoceaceae)), (zosteraceae, potamogetonaceae)))))))) alismatales)narthecidae, (acoraceae)acorales)monocots, ((ceratophyllaceae)ceratophyllales, ((eupteleaceae, (((lardizabalaceae, circaeasteraceae)lardizabalaceae_to_circaeasteraceae, (menispermaceae, (berberidaceae, ranunculaceae)ranunculaceae_to_berberidaceae)), papaveraceae))ranunculales, (sabiaceae, (nelumbonaceae, (platanaceae, (((((((((macadamia_grandis, macadamia_claudiensis), macadamia_whelanii), ((orites_megacarpus, panopsis), brabejum)), ((macadamia_integrifolia, macadamia_tetraphylla), (macadamia_ternifolia, macadamia_jansenii))), ((malagasia, catalepidia), ((heliciopsis, athertonia), virotia))), (cardwellia, ((euplassa, (sleumerodendron, (turrillia, kermadecia))), gevuina, (bleasdalea, hicksbeachia)))))), (((floydia, lambertia), (roupala, orites_diversifolius)), ((((((banksia_ilicifolia, banksia_oligantha), banksia_cuneata)isostylis, banksia_elegans, banksia_attenuata), (banksia_candolleana, ((banksia_menziesii, banksia_burdetii, banksia_victoriae, (banksia_hookeriana, banksia_prionotes)), (banksia_sceptrum, banksia_ashbyi), (banksia_lindleyana)lindleyanae)), (dryandra_sessilis, dryandra_serratuloides, dryandra_foliosissima, dryandra_calophylla, dryandra_speciosa)dryandra, ((banksia_baxteri, banksia_speciosa), banksia_coccinea)), ((((banksia_lemanniana, banksia_caleyi, banksia_aculeata), banksia_elderiana, banksia_baueri, banksia_lullfitzii, (banksia_repens, banksia_chamaephyton, banksia_blechnifolia, banksia_goodii), banksia_hiemalis, banksia_petiolaris, banksia_brevidentata), (banksia_benthamiana, banksia_audax), banksia_laevigata, (banksia_ornata, banksia_serrata, banksia_aemula)), (banksia_pilostylis, banksia_media, banksia_epica, banksia_praemorsa)cyrtostylis))cryptostomata, (((banksia_dentata, ((banksia_oblongifolia, banksia_robur), banksia_plagiocarpa, banksia_integrifolia_aquilonia), (banksia_integrifolia_integrifolia, banksia_integrifolia_monticola, banksia_integrifolia_compar, (banksia_marginata, banksia_saxicola), banksia_paludosa), banksia_canei)salicinae, ((banksia_spinulosa_spinulosa, (banksia_spinulosa_collina, banksia_spinulosa_neoanglica), banksia_spinulosa_cunninghamii), banksia_ericifolia_ericifolia)), (((banksia_occidentalis, banksia_littoralis), banksia_brownii, banksia_verticillata), (banksia_nutans_nutans, banksia_nutans_cernuella)), (banksia_quercifolia, banksia_oreophila)quercinae, (((((banksia_telmatiaea, banksia_scabrella, banksia_leptophylla_melletica, banksia_leptophylla_leptophylla, banksia_lanata), banksia_grossa), (banksia_micrantha, (banksia_sphaerocarpa_sphaerocarpa, banksia_sphaerocarpa_caesia)), (banksia_dolichostyla, banksia_violacea, (banksia_laricina, banksia_incana))), banksia_tricuspis), ((banksia_pulchella, banksia_meisneri_cendens), (banksia_dry

androides)dryandroideae), (banksia_grandis, banksia_solandri)grandes))phanerostomata)banksia)), carnarvonia), grevillea)proteaceae)plat-anaceae_to_proteaceae)proteales, ((buxaceae, haptanthaceae)buxales, (trochodendraceae)trochodendrales, ((gunneraceae, myrotham-naceae)gunnerales, ((((((((((anisophylleaceae, ((coriariaceae, corynocarpaceae), (cucurbitaceae, (tetramelaceae, (begoniaceae, datisca-ceae)))))cucurbitales, (nothofagaceae, (fagaceae, ((myricaceae, juglandaceae)juglandaceae_to_myricaceae, (casuarinaceae, (ticodendraceae, (((((ostrya_rehderiana, ostrya_virginiana)ostrya, (((carpinus_putoensis, carpinus_hupeana), (carpinus_polyneura, carpinus_turczaninowii)), carpinus_cordata)carpinus, ostryopsis_davidiana), (corylus_heterophylla, corylus_chinensis)corylus)coryloideae, ((betula_alleghaniensis, (betula_glandulosa, betula_pendula))betula, (((alnus_glutinosa, alnus_incana), alnus_crispa), alnus_maritima)alnus)betuloideae))betu-laceae)))))fagales)fagales_to_cucurbitales, (((((((adenostoma, (chamaebatiaria, (sorbaria, spiraeanthus)))sorbarieae, (((((((((amelanchier, peraphyllum), malacomeles), (crataegus, mespilus)), aria, aronia, (chaenomeles, osteomeles), ((chamaemeles, malus), cotoneaster), (chamaemespilus, torminalis), cormus, (cydonia, (photinia, pseudocydonia)), dichotomanthes, docyniopsis, ((((eriobotrya, rhaphiolepis), het-eromeles), pyrus), stranvaesia), eriolobus, pyracantha, sorbus)pyrinae), vauquelinia), (kageneckia, lindleya))pyreae, gillenia)pyrodae, (((arun-cus, luetkea), holodiscus), ((kelseya, petrophyton), spiraea))spiraeeae), (((coleogyne, kerria, neviusia), rhodotypos)kerrieae, (exochorda, (oemleria, prinsepia))osmaronieae)kerriodae), ((maddenia, pygeum, prunus)amygdaleae, (neillia, physocarpus)neillieae)), lyonothamnus)spi-raeoideae, ((cercocarpus, (chamaebatia, cowania, purshia)), dryas)dryadoideae)rosaceae, ((barbeyaceae, (dirachmaceae, ((((sageretia, scutia), (rhamnus, frangula), (rhamnella, krugiodendron, rhamnidium, (karwinskia, condalia), reynosia, berchemia)rhamneae), maesopsis), ventilago)rhamnoids, ((bathiorhamnus, ampeloziziphus, doerpfeldia)ampeloziziphoids, ((hovenia, (paliurus, ziziphus))paliureae, ceanothus, (spyridium, (trymalium, (pomaderris, siegfriedia)), cryptandra)pomaderreae, (phylica, (nesiota, noltea))phyliceae, schistocarpaea, ((discaria, (adolphia, trevoa)), colletia)colletieae, colubrina, alphitonia, emmenosperma, lasiodiscus, ((gouania, helinus), (reissekia, (crumenaria, pleuranthodes))gouanieae))ziziphoids))rhamnaceae, elaeagnaceae)), (ulmaceae, (cannabaceae, ((((((((((antiaris_toxicaria)antiaris, (mesogyne_insignis)mesogyne), ((((((castilla_elastica, castilla_ulei)castilla, (helicostylis_pedunculata, helicostylis_tomentosa)helicostylis), ((perebea_angustifolia, perebea_humilis), perebea_longepedunculata), perebea_rubra, perebea_xanthochyma), (maquira_costaricana)maquira), ((pseudolmedia_laevigata, (pseudolmedia_laevis, pseudolmedia_macrophylla)), pseudolmedia_spuria)pseudolmedia), (((naucleopsis_caloneura, naucleopsis_ternstroemiifolia), naucleopsis_guianensis), ((naucleopsis_krukovii, naucleopsis_ulei), naucleopsis_naga))naucleopsis)), (poulsenia_armata)poulsenia), ((antiaropsis_decipiens)antiaropsis, (sparratosyce_dioca)sparratosyce)), (((((ficus_asperula, (ficus_copiosa, ficus_wassa)), (ficus_racemosa, ficus_variegata)), ficus_virens), (ficus_edelfeltii, ficus_habrophylla)), ficus_insipida)ficus), (((((bleekrodea_madagascariensis)bleekrodea, streblus_elongatus), ((((brosimum_alicastrum, brosimum_utile), ((brosimum_guianense, brosimum_rubescens), (helianthostylis_sprucei)helianthostylis, (trymatococcus_amazonicus, trymatococcus_oligandrus)trymatococcus)), brosimum_lactescens), ((dorstenia_bahiensis, dorstenia_choconiana)dorstenia, (utsetela_neglecta)utsetela))), ((brousonettia_papyrifera)brousonettia, trophis_scandens)), (fatoua_pilosa)fatoua)), ((maclura_amboinensis, maclura_tricuspidata), maclura_pomifera)maclura), (((((artocarpus_altilis, artocarpus_heterophyllus), artocarpus_vrieseanus)artocarpus, ((parartocarpus_venenosus)parartocarpus, (prainea_limpato, prainea_papuana)prainea)), (batocarpus_amazonicus, (batocarpus_costaricensis, (clarisia_biflora, clarisia_ilicifolia)clarisia))), (((bagassa_guianensis)bagassa, (((milicia_excelsa)milicia, ((streblus_glaber, streblus_pendulinus), streblus_smithii)), ((morus_alba, morus_nigra)morus, (trophis_involucrata, trophis_racemosa)trophis))), (((sorocea_affinis, sorocea_pubivena), sorocea_briquetii), sorocea_bonplandii)sorocea)))moraceae, urticaceae)cannabaceae_to_moraceae))))rosales), (quillajaceae, (((bauhinia, cercis)cercideae, (((((berlinia, brachystegia, oddoniodendron), brownea, cynometra, amherstia), ((hymenaea, guibourtia, peltogyne), tessmannia)), (barnebydendron, goniorrhachis), schotia, (colophospermum, prioria))detarieae, (((((dialium, martiodendron), petalostylis), apuleia), poeppigia)dialiinae, ((((arcoa, ceratonia, gymnocladus, gleditsia)umtiza_clade, diptychandra, (((chamaecrista, cassia, senna)cassiinae, (((hoffmannseggia, zuccagnia), (caesalpinia, libidibia, cenostigma, pomaria, poincianella, guilandia, stuhlmannia, haematoxylum, erythrostemon))caesalpinia_group, pterogyne)pterogyne_group), (tachigali, ((conzattia, parkinsonia, peltophorum)core_peltophorum_group, ((mora, dimorphandra, erythrophleum)dimorphandra_group, (dinizia, pentaclethra, mimozyganthus, ((amblygonocarpus, adenanthera, tetrapleura, xylia, pseudoprosopis, calpocalyx)adenanthera_group, (piptadeniastrum, (entada, (plathymenia, ((neptunia, prosopis, prosopidastrum)prosopis_group, (desmanthus, leucaena)leucaenae_group, (dichrostachys, gagnebina)dichrostachys_group, (parkia, (microlobius, parapiptadenia, stryphnodendron, anadenanthera, pseudopiptadenia, adenopodia, piptadenia, mimosa)piptadenia_group, (acacia, ((faidherbia, zapoteca), lysiloma, enterolobium, albizia, ((chloroleucon, leucochloron, blanchetiodendron)chloroleucon_alliance, (abarema, pararchidendron)abarema_alliance, (samanea, pseudosamanea)samanea_alliance, (havardia, ebenopsis, pithecellobium)pithecellobium_alliance, (calliandra, cojoba, zygia, macrosamanea, cedrelinga, archidendron, inga)inga_alliance))ingeae)))))))))mimosoids))))), ((((swartzia, bobgunnia, bocoa, candolleodendron), (trischidium, cyathostegia, ateleia)), ((((amburana, mildbraediodendron, cordyla, aldina), (dussia, myrocarpus, myroxylon, myrospermum, monopteryx)), ((dipteryx, pterodon), taralea)), (xanthocercis, angylocalyx, castanospermum, alexa), (((styphnolobium, pickeringia), cladrastis), (((calia, uribea), (zollernia, holocalyx, lecointea)), ((sweetia, luetzelburgia, vatairea, vataireopsis), (harleyodendron, exostyles)), ((hymenolobium, andira), (((apoplanesia, ((parryella, amorpha), (errazurizia, eysenhardtia))), ((psorodendron, psorothamnus), (marina, dalea)))amorpheae, ((adesmia, amicia, zornia, poiretia, nissolia, chaetocalyx)adesmia_group, (((riedeliella, discolobium), ((cranocarpus, brya), platymiscium, (platypodium, inocarpus, maraniona, tipuana, ramorinoa, centrolobium, paramachaerium, etaballia, pterocarpus), (cascaronia, geoffroea), (fissicalyx, fiebrigiella, chapmannia, stylosanthes, arachis), grazielodendron))pterocarpus_group, ((dalbergia, machaerium, aeschynomene_a), (aeschynomene_b, cyclocarpa, soemmeringia, smithia, kotschya, humularia, bryapsis, geissaspis), (pictetia, diphysa, zygocarpum, ormocarpum, ormocarpopsis, peltiera), weberbauerella)dalbergia_group))dalbergieae)), ((((cyclolobium, poecilanthe), tabaroa, (harpalyce, ((brongniartia, plagiocarpus), ((templetonia, hovea), (cristonia, (thinicola, lamprolobium)))))), ((euchresta, ((ammopiptanthus, (anagyris, piptanthus)), (thermopsis, baptisia)), ((ammondendron, ammothamnus, maackia, sophora_ss, salweenia), camoensia)), ((cyclopia, ((xiphotheca, amphithalea), (stirtonanthus, (podalyria, (liparia, (virgilia, calpurnia)))))), ((spartidium, (lebeckia, wiborgia, rafnia, aspalathus), ((lotononis, bolusia, crotalaria), (pearsonia, rothia, robynsiophyton)))crotalarieae, ((melolobium, dichilus, polhillia), (argyrolobium_a, ((lupinus, anarthrophyllum, sellocharis), (argyrolobium_b, (adenocarpus, ((cytisophyllym, argyrocytisus, petteria, laburnum, podocytisus, hesperolaburnum, cytisus, lembotropis, calicotome), (echinospartum, erinacea, retama, gonocytisus, genista, spartium, stauracanthus, ulex)))))))genisteae)))), (ormosia, haplormosia, pericopsis, acosmium, bowdichia, diplotropis, clathotropis, petaladenium, sakoanala, neoharmsia, bolusanthus, platycelyphium, dicraeopetalum, cadia)ormosieae)genistoids, (((baphia, baphiastrum, bowringia, leucomphalos, airyantha, dalhousiea), baphiopsis)baphieae, ((hypocalyptus, ((goodia, ((bossiaea, platylobium), (muelleranthus, (ptychosema, aenictophyton)))), gompholobium, sphaerolobium, ((daviesia, erichsenia), viminaria), (isotropis, (jacksonia, leptosema, latrobea, euchilopsis, phyllota, otion, aotus, urodon, stonesiella, almaleea, eutaxia, dillwynia, pultenaea, mirbelia, chorizema, oxylobium, podolobium, callistachys, gastrolobium))))mirbelieae, (((((((callerya, endosamara, sarcodum, afgekia, antheroporum), wisteria), glycyrrhiza), ((((erophaca, ((oxytropis, (astragalus, (biserrula, (ophiocarpus, barnebyella)))))), (((colutea, ((oreophysa, smirnowia, eremosparton), sphaerophysa)), (lessertia, sutherlandia)), (swainsona, (clianthus, (montigena, carmichaelia), streblorrhiza))))), (chesneya, spongiocarpella, (gueldenstaedtia, tibetia))), (((caragana, halimodendron), calophaca), (alhagi, (eversmannia, (hedysarum, corethrodendron, sulla, taverniera), (onobrychis, sartoria, ebenus))))), (parochetus, (galega, (cicer, (((trifolium, ((lathyrus, (pisum, vavilovia)), ((lens, viciaa), viciab))), ((melilotus, trigonella), medicago)), ononis)))))irlc, (((hebestigma, lennea), ((gliricidia, poitea), (((olneya, (poissonia, sphinctospermum)), (coursetia, (peteria, genistidium))), robinia)))robinieae, (sesbania, (((lotus, dorycnium, tetragonolobus), (hammatolobium, cytisopsis, tripodion)), (((coronilla, securigera), scorpiurus), hippocrepis), (anthyllis, hymenocarpos), (((acmispon, syrmatium), ottleya), (dorycnopsis, (kebirita, (ornithopus, hosackia)))), antopetitia, pseudolotus, pod

olotus)loteae))), ((phylloxylon, ((((rhynchotropis, microcharis), indigastrum), cyamopsis), (vaughania, indigofera)))indigofereae, ((austrosteenisia, leptoderris, dalbergiella, aganope, ostryocarpus, xeroderris, fordia_ss, platysepalum, sylvichadsia, schefflerodendron, craibia, disynstemon, platycyamus, kunstleria, burkilliodendron, craspedolobium), (abrus, (((dioclea, luzonia, macropsychanthus, canavalia, cymbosema, cleobulia, camptosema, cratylia, galactia, collaea, lackeya, rhodopis, neorudolphia), ((cruddasia, ophrestia), pseudoeriosema))galactinae, (((fordia_pp, millettia_pp), philenoptera), ((hesperothamnus, piscidia), ((dahlstedtia, deguelia, lonchocarpus, behaimia, bergeronia, margaritolobium, muellera), (derris, paraderris), (millettia_ss, pongamiopsis), (pyranthus, chadsia, mundulea, tephrosia, apurimacia, paratephrosia, requienia, ptycholobium))))millettioids)), ((((((((((otholobium, psoralea), ((orbexilum, hoita), (rupertia, psoralidium, (pediomelum, (bituminaria, cullen)))))psoraleeae, calopogonium, cologania, pachyrhizus, herpyza, neorautanenia, neonotonia, teyleria, dumasia, pueraria, nogra, eminia, sinodolichos, pseudeminia, pseudovigna, amphicarpaea, teramnus, glycine, phylacium, neocollettia)glycininae, (wajira, shenostylis, nesphostylis, alistilus, austrodolichos, dolichos, macrotyloma, spathionema, vatovaea, physostigma, ((dipogon, lablab), (vigna, oxyrhynchus, phaseolus, ramirezella, ((strophostyles, dolichopsis), macroptilium, mysanthus, oryxis))))phaseolinae), (erythrina, psophocarpus, dysolobium, otoptera, descorea)erythrininae, strongylodon), (adenodolichos, paracalyx, bolusafra, carrissoa, chrysoscias, rhynchosia, eriosema, dunbaria, cajanus, flemingia)cajaninae), (spatholobus, butea, meizotropis)), ((apios, cochlianthus, shuteria, mastersia, diphyllarium), ((mucuna, (((campylotropis, kummerowia), lespedeza), ((dendrolobium, phyllodium, ougeinia, aphyllodium, ohwia, hanslia, arthroclianthus, nephrodesmus, tadehagi, akschindlium, droogmansia), (monarthrocarpus, trifidacanthus, desmodium, codariocalyx, hylodesmum, hegnera, pseudarthria, pycnospora, mecopus, uraria, christia, alysicarpus, desmodiastrum, meliniella, leptodesmia, eliotis)))desmodieae), (kennedia, hardenbergia, vandasina)kennedinae))), (barbieria, clitoria, centrosema, periandra, clitoriopsis)clitorinae)phaseoloids)))))))))papilionoideae))))fabaceae, (surianaceae, polygalaceae)))fabales)nitrogenfixing, ((lepidobotryaceae, celastraceae)celastrales, ((huaceae, ((connaraceae, oxalidaceae), ((((((((((weinmannia, (cunonia, pancheria)), vesselowskya), ((callicoma, codia), pullea)), (((ackama, spiraeopsis), opocunonia), caldcluvia), ((geissois, pseudoweinmannia), lamanonia), acrophyllum, gillbeea, aistopetalum, eucryphia), bauera), (((anodopetalum, platylophus), ceratopetalum), schizomeria)), davidsonia), (acsmithia, spiraeanthemum))cunoniaceae, ((brunelliaceae, cephalotaceae), elaeocarpaceae))))oxalidales, ((achariaceae, goupiaceae, violaceae, passifloraceae), (lacistemataceae, salicaceae))), centroplacaceae, caryocaraceae, (rafflesiaceae, euphorbiaceae), humiriaceae, irvingiaceae, ixonanthaceae, linaceae, (putranjivaceae, lophopyxidaceae), pandaceae, (phyllanthaceae, picrodendraceae), (ctenolophonaceae, (erythroxylaceae, rhizophoraceae)), ((bonnetiaceae, clusiaceae), (calophyllaceae, (hypericaceae, podostemaceae))), (malpighiaceae, elatinaceae), ochnaceae, (balanopaceae, ((trigoniaceae, dichapetalaceae), (chrysobalanaceae, euphroniaceae))))malpighiales))celastrales_to_malpighiales), (zygophyllaceae, krameriaceae)zygophyllales)fabids, (((((((neuradaceae, (thymelaeaceae, (sphaerosepalaceae, bixaceae, (cistaceae, (sarcolaenaceae, dipterocarpaceae))sarcolaenaceae_to_dipterocarpaceae, (cytinaceae, muntingiaceae), malvaceae)))malvales, ((akaniaceae, tropaeolaceae), ((caricaceae, moringaceae)moringaceae_to_caricaceae, (setchellanthaceae, (limnanthaceae, ((koeberliniaceae, (bataceae, salvadoraceae)), (emblingiaceae, (pentadiplandraceae, (gyrostemonaceae, resedaceae), tovariaceae, (capparaceae, (cleomaceae, brassicaceae)brassicaceae_to_cleomaceae))))))))brassicales)malvales_to_brassicales, (gerrardinaceae, (dipentodontaceae, tapisciaceae))huerteales)huerteales_to_brassicales, (biebersteiniaceae, (nitrariaceae, ((kirkiaceae, (anacardiaceae, burseraceae)bursa_to_anaca), (sapindaceae, (simaroubaceae, ((((((aglaia, aphanamixis, lansium, dysoxylum, guarea, heckeldora, ruagea, synoum), (((calodecaryia, turraea), nymania), munronia, cipadessa, malleastrum, trichilia)), walsura), (ekebergia, quivisianthe)), (azadirachta, melia)melieae)melioideae, (((((capuronianthus, lovoa), (carapa, khaya, swietenia)), (cedrela, toona)), neobeguea), (chukrasia, schmardaea))swietenioideae)meliaceae, rutaceae)meliaceae_to_rutaceae))))sapindales), (picramniaceae)picramniales), ((staphyleaceae, (guamatelaceae, (stachyuraceae, crossosomataceae)crossosomataceae_to_stachyuraceae)), (aphloiaceae, (geissolomataceae, strasburgeriaceae)))crossosomatales), ((combretaceae, ((onagraceae, lythraceae), ((((((((((((((((((neomitranthes_cordifolia, siphoneugena), plinia_pauciflora), myrciaria)pliniagroup, algrizea_macrochlamys), ((calyptranthes, (marlierea_eugeniopsoides, myrcia1), myrcia2, myrcia3), ((marlierea, myrcia_multiflora, myrcia), myrcia_racemosa), myrcia4, myrcia_bicarinata)myrciagroup), ((blepharocalyx_cruckshanksii, luma), myrceugenia)myrceugeniagroup), (((((neomyrtus_pedunculata, lophomyrtus_obcordata), lophomyrtus_bullata), ugni_mollinae), myrteola_nummularia)myrteolagroup, ((((((campomanesia, psidium), acca_sellowiana, myrrhinium_atropurpureum), pimenta), (amomyrtus, legrandia_concinna))pimentagroup, (eugenia, myrcianthes)eugeniagroup))), blepharocalyx_salicifolius), ((rhodamnia, (decaspermum_humile, (octamyrtus_pleiopetala, rhodomyrtus_psidioides))), (gossia, austromyrtus_dulcis))australasiangroup), myrtus_communis)myrteae, ((syzigium, backousieae), (metrosidereae, tristanieae)), (tristaniopsis, sphaerantia)kanieae)myrteaestem, ((((((chamelaucium, homoranthus)chamelaucieae, micromyrtus), (homalocalyx, calytrix)), leptospermeae), (eucalypteae, syncarpieae)eucalypteaestem), lindsayomyrtus)), ((((beaufortia, calothamnus), melaleuca), callistemon), osbornia)), (xanthostemom, (kjellbergiodendron, lophostemon))), (heteropyxis, psiloxylum)psiloxydeae)myrtaceae, vochysiaceae), (melastomataceae, (crypteroniaceae, (alzateaceae, penaeaceae))))))myrtales, (geraniaceae, (melianthaceae, vivianiaceae))geraniales))malvids), (vitaceae)vitales)rosids, (peridiscaceae, ((paeoniaceae, (altingiaceae, (hamamelidaceae, (cercidiphyllaceae, daphniphyllaceae)))), ((crassulaceae, (aphanopetalaceae, (tetracarpaeaceae, (penthoraceae, haloragaceae)penthoraceae_to_haloragaceae))), (iteaceae, (grossulariaceae, saxifragaceae)))))saxifragales)subrosid, dilleniaceae, ((aextoxicaceae, berberidopsidaceae)berberidopsidales, ((balanophoraceae, olacaceae, (((misodendraceae, schoepfiaceae), loranthaceae), (opiliaceae, santalaceae)))santalales, ((((droseraceae, (nepenthaceae, (drosophyllaceae, (ancistrocladaceae, dioncophyllaceae)dioncophyllaceae_to_ancistrocladaceae))), ((tamaricaceae, frankeniaceae), (polygonaceae, plumbaginaceae)plumbaginaceae_to_polygonaceae)), (rhabdodendraceae, (simmondsiaceae, ((asteropeiaceae, physenaceae), ((amaranthaceae, achatocarpaceae, caryophyllaceae)amaranthaceae_to_caryophyllaceae, (stegnospermataceae, (limeaceae, ((lophiocarpaceae, (barbeuiaceae, ((((((trianthema_portulacastrum, (trianthema_turgidifolia, (trianthema_cussackiana, (trianthema_compacta, trianthema_glossistigma, trianthema_oxycalyptra, (trianthema_patellitecta, (trianthema_rhynchocalyptra, (trianthema_megasperma, trianthema_pilosa)))))))), zaleya), (trianthema_triquetra, (trianthema_parvifolia, (trianthema_sheilae, trianthema_triquetra_africa)))), ((cypsela, (sesuvium_maritimum, sesuvium_portulacastrum, sesuvium_sessile, sesuvium_verrucosum)sesuvium), (sesuvium_sesuviodes, sesuvium_hydaspicum))), mesembryanthemum)aizoaceae, (nyctaginaceae, gisekiaceae, sarcobataceae, phytolaccaceae))), (molluginaceae, ((((anacampserotaceae, cactaceae), portulacaceae)cactaceae_to_portulaceae, talinaceae), halophytaceae, didiereaceae, montiaceae, basellaceae)))))))))caryophyllales, ((hydrostachyaceae, ((loasaceae, hydrangeaceae), cornaceae, (curtisiaceae, grubbiaceae)))cornales, (((balsaminaceae, (marcgraviaceae, tetrameristaceae)), (((polemonioideae, cobaeoideae, acanthogilioideae)polemoniaceae, fouquieriaceae), lecythidaceae, ((sladeniaceae, pentaphylacaceae), (sapotaceae, (ebenaceae, primulaceae)), (mitrastemonaceae, theaceae, (symplocaceae, (styracaceae, diapensiaceae)styracaceae_to_diapensiaceae), (((actinidiaceae, roridulaceae), sarraceniaceae), (clethraceae, (cyrillaceae, (enkianthoideae, (monotropoideae, (arbutoideae, ((cassiopoideae, ericoideae)cassiopoideae_to_ericoideae, (harrimanelloideae, (styphelioideae, vaccinioideae)styphelioideae_to_vaccinioideae)harrimanelloideae_to_vaccinioideae)cassiopoideae_to_vaccinioideae)arbutoideae_to_vaccinioideae)monotropoideae_to_vaccinioideae)ericaceae)))))))ericales, ((icacinaceae, metteniusaceae, oncothecaceae, (garryaceae, eucommiaceae)garryales, ((((((pauridiantha, amphidasya), (ophiorrhiza, ((hindsia, (coussarea, faramea)), (schradera, ((psychotria, palicourea), morinda)), (pentanisia, (serissa, paederia), hedyotis, (theligonum, rubia), mycetia, nertera))))rubioideae, luculia, (((bathysa_veraguensis, bathysa, condaminea, dioicodendron, elaeagia, emmenopterys, hippotis, macbrideina, parachimarrhis, pentagonia, picardaea, pinckneya, pogonopus, rustia, simira, sommera, wittmackanthus, ((chimarrhis_hookeri, chimarrhis_glabriflora), chimarrhis_turbinata, chimarrhis_microcarpa, capirona, dolicodelphys, warszewiczia), (calycophyllum, alseis)), ((mussaenda, pseudomussaenda), (retiniphyllum, (((vangueria, (keetia, psydrax)), (greenea, ((aleisanthiopsis, aleisanthia), ixora))), ((wendlandia, (augusta_rivalis, augusta_longifolia)augusta), ((randia, (genipa, gardenia)), duroia, ((tarenna, pavetta), (tricalysia, coffea), bertiera), (didymosalpinx, paragenipa)))))), ((maguireothamnus,

(((sipanea_biflora, sipanea_stahelii), sipanea_pratensis)sipanea, (sipaneopsis, neobertiera))), ((posoqueria, molopanthera), gleasonia)))ixoroideae, ((ladenbergia, cinchona), (((hoffmannia, hamelia), cosmibuena), chione), (isertia_hypoleuca, isertia_coccinea)isertia, ((uncaria, sarcocephalus), cephalanthus), ((coutaportia_ghiesbreghtiana, coutaportia_guatemalensis, hintonia, exostema_lineatum, exostema_purpureum, erithalis, (coutarea_andrei, coutarea_hexandra)coutarea, ((cubanola, ((portlandia, (isidorea_pedicellaris, isidorea_pungens)isidorea), (catesbaea_parviflora, (catesbaea_spinosa, phyllacanthus)))), ((bikkia, badusa, siemensia, (schimidtottia, (phialanthus, ceratopyxis))), (scolosanthus, (chiococca, asemnantha))))), strumpfia), ((((rogiera_amoena, rogiera_cordata)rogiera, (neoblakea, machaonea, allenanthus), ((guettarda_speciosa, guettarda_ferruginea, timonius, antirhea, (guettarda_crispiflora, chomelia), (guettarda_boliviana, guettarda_odorata)guettarda), (javorkaea, gonzalagunea_veraguensis, arachnothryx_laniflora, arachnothryx_fosbergii, arachnothryx_leucophylla, (gonzalagunia_dicocca, gonzalagunia_rosea, gonzalagunia_kallunkii)gonzalagunia))), (blepharidium, (suberanthus_stellatus, suberanthus_neriifolius)suberanthus, (acrosynanthus, (roigella, rachicallis, (phyllomelia, mazaea_phialanthoides, mazaea_shaferi), (rondeletia_sp1, (rondeletia_alaternoides, rondeletia_odorata), (rondeletia_intermixta, rondeletia_portoricensis, rondeletia_pilosa, rondeletia_inermis))rondeletia))))))cinchonoideae))rubiaceae, (gentianaceae, (loganiaceae, (gelsemiaceae, ((alstonia_scholaris)alstonieae, (((kopsia_fruticosa, rauvolfia_mannii)vinceae, (molongum_laxum, tabernaemontana_divaricata)tabernaemontaneae), ((((chilocarpus_suaveolens)alyxieae), picralima_nitida), ((thevetia_peruviana, (allamanda_cathartica, plumeria_rubra)), (acokanthera_oblongifolia, (nerium_oleander, (strophanthus_divaricatus, ((beaumontia_grandiflora, apocynum_androsaemifolium), ((((raphionacme_welwitschii, schlechterella_abyssinica), ((hemidesmus_indicus, cryptostegia_grandiflora), (periploca_graeca, camptocarpus_mauritianus)))periplocoideae, (((((secamone_bosseri, secamone_cristata), (secamone_buxifolia, (secamone_sparsiflora, secamone_uncinata)), secamone_falcata, secamone_elliottii, secamone_parvifolia, secamone_geayii, (secamone_minutifolia, secamone_ecoronata))secamone, (pervillaea_venenata, pervillaea_phillipsonii), (secamonopsis_microphylla, secamonopsis_madagascariensis)secamonopsis, secamone_volubilis)secamonoideae, (fockea_capensis, ((riocreuxia_burchellii, dregea_sinensis), (pergularia_daemia, (pentarrhinum_insipidum, ((vincetoxicum_nigrum, tylophora_indica), (araujia_sericifera, (gonolobus_xanthotricus, matelea_quirosii)gonolobeae))))))asclepiadoideae)))))))))))apocynaceae))))gentianales, ((plocospermataceae, ((oleaceae, carlemanniaceae), (tetrachondraceae, ((calceolariaceae, gesneriaceae), (plantaginaceae, (scrophulariaceae, (stilbaceae, ((((((((((salvia_africana_caerulea, salvia_aurita), salvia_brachyantha, salvia_nilotica, salvia_taraxicifolia, salvia_verticillata), ((salvia_henryi, salvia_summa), salvia_roemeriana), salvia_aethiopis, (salvia_argentea, salvia_indica), (salvia_bucharica, salvia_canariensis), (salvia_cadmica, salvia_candidissima), (salvia_penstemonoides, salvia_texana), salvia_amplexicaulis, salvia_candelabrum, salvia_disermis, salvia_verbenaca, salvia_lavandulifolia, salvia_lyrata, salvia_officinalis, salvia_palestina, salvia_pratensis, salvia_ringens, salvia_sclarea, salvia_sylvestris, salvia_staminea, salvia_viridis, salvia_viscosa, ((monarda_didyma, monarda_fistulosa), monarda_menthaefolia) monarda, origanum_laevigatum, origanum_vulgare, (thymus_alsinoides, thymus_vulgaris) thymus, majorana_hortensis, mentha_longifolia, mentha_rotundifolia), rosmarinus_officinalis), (perovskia_abrotanoides, perovskia_atriplicifolia)perovskia), (((salvia_fruticosa, salvia_glutinosa), salvia_nubicola), ((salvia_digitaloides, salvia_barrelieri), salvia_hians))), (((((((((salvia_polystachya, salvia_tiliifolia), salvia_farinacea), (salvia_coccinea, salvia_hirsuta), salvia_cedrocensis), salvia_involucrata), (salvia_amarissima, salvia_lycioides, salvia_microphylla)), salvia_chamaedryoides, salvia_divinorum, salvia_greggii, salvia_guaranitica, salvia_misella, salvia_section_biflorae), (((salvia_elegans, salvia_uliginosa), salvia_corrugata), salvia_subincisa), salvia_ballotiflora), salvia_cf.sagittata)calosphace, (((salvia_brandegei, salvia_dorrii, salvia_pachyphylla, salvia_spathacea), (salvia_chionopeplica, salvia_clevelandii, salvia_eremostachya)), salvia_columbariae), (salvia_californica, salvia_greatai), dorystaechas_hastata), ((((((dracocephalum_grandiflorum, dracocephalum_moldavica), dracocephalum_ruyschiana)dracocephalum, (satureja_hortensis, satureja_montana)satureja), ((agastache_foeniculum, agastache_mexicana, agastache_rugosa)agastache, glechoma_hederacea)), ((nepeta_cataria, nepeta_tuberosa), nepeta_faassenii)nepeta), horminum_pyrenaicum), ((((prunella_grandiflora, prunella_hyssopifolia), prunella_vulgaris)prunella, lepechinia_chamaedryoides), (lepechinia_calycina, lepechinia_fragrans)), (melissa_officinalis, ocimum_basilicum)), (((((lavandula_angustifolia, lavandula_stoechas), lavandula_latifolia), lavandula_lanata)lavandula, plectranthus_barbatus), collinsonia_canadensis)), (((((marrubium_incanum, marrubium_peregrinum), marrubium_vulgare)marrubium, (lamium_amplexicaule, lamium_garganicum), lamium_album), lamium_galeobdolon, lamium_maculatum, lamium_purpureum, stachys_lavandulaefolia), (caryopteris_bicolor, trichostema_dichotomum), vitex_agnuscastus, westringia_rosmariniformis))lamiaceae, (phrymaceae, orobanchaceae, paulowniaceae)), ((thomandersiaceae, verbenaceae), (acanthaceae, bignoniaceae, byblidaceae, linderniaceae, lentibulariaceae, martyniaceae, pedaliaceae, schlegeliaceae)))))))))lamiales, ((montiniaceae, (hydroleaceae, sphenocleaceae)), (convolvulaceae, ((((((((((((((((((((brevantherum, geminata), leptostemonum), unclear1), unclear2), cyphomandra), unclear3), (((dulcamaroid, morelloid), ((normania, archeosolanum), africannonspiny)), potatoe, regmandra)), thelopodium)solanum, jaltomata)solaneae, (((capsicum, lycianthes2), lycianthes1)capsiceae, (((((((physalis2, margaranthus_solanaceus), chamaesaracha), quincula_lobata), oryctes_nevadensis, physalis1, leucophysalis, (((witheringia1, brachistus_stramonifolius), witheringia_solanacea), witheringia_mexicana))physalinae, (((acnistus_arborescens, iochroma_australe, eriolarynx_lorentzii, vassobia_dichotoma), saracha_punctata, iochroma_fuchsioides, iochroma_umbellatum, dunalia_solanacea)iochrominae, larnax)), ((withamia, mellissia_begonifolia), (aureliana_fasciculata, athenaea_sp), ((tubocapsicum_anomalum, nothocestrum), discopodium_penninervum))withaninae), (cuatresia_riparia, (cuatresia_exiguiflora, witheringia_cuneata)))physaleae, (salpichroa_origanifolia, nectouxia_formosa))), (datura, brugmansia, iochroma_cardenasianum)datureae), mandragora), ((((markea, merinthopodium_neuranthum, juanulloa_mexicana), dyssochroma_viridiflora)juanulloeae, solandra), schultesianthus)), nicandra_physalodes), exodeconus_miersii), ((atropa, (anisodus, ((atropanthe_sinensis, (physochlaina, scopolia_carniolica, (scopolia_japonica, przewalskia_tangutica))), hyoscyamus)))hyoscyameae, (((grabowskia, lycium_cestroides, phrodus_microphyllus, lycium_sandwicense), lycium_barbarum, lycium_pallidum)lycieae, nolana, sclerophylax), jaborosa, latua_pubiflora))solanoideae, (((((((((cyphanthera_albicans, duboisia_myoporoides), duboisia_leichhardtii, duboisia_hopwoodii), cyphanthera_anthocercidea), crenidium_spinescens), cyphanthera_microphylla), anthotroche), (cyphanthera_odgersii, grammosolen)), anthocercis), symonanthus, nicotiana)nicotianoideae), (schwenckia, melananthus_guatemalensis)schwenckieae, ((((((plowmania_nyctaginoides, hunzikeria_texana), bouchetia_erecta), nierembergia), leptoglossis_darcyana), brunfelsia), (petunia_axillaris, (calibrachoa_parviflora, fabiana_imbricata)))petunieae, ((benthamiella_skottsbergii, (combera_paradoxa, pantacantha_ameghinoi))benthamielleae, (salpiglossis_sinuata, (((streptosolen_jamesonii, browallia_eludens), browallia_speciosa) browallieae, (protoschwenckia_mandonii, (vestia_foetida, (sessea_corymbiflora, cestrum))cestreae)))cestroideae)), duckeodendron_cestroides, (((goetzea, espadaea_amoena, henoonia_myrtifolia), coeloneurum_ferrugineum), (tsoala_tubiflora, metternichia_principis))goetzeoideae), schizanthus)solanaceae)solanaceae_to_convolvulaceae)solanales), boraginaceae))lamiids, (((stemonuraceae, cardiopteridaceae), (phyllonomaceae, (helwingiaceae, aquifoliaceae)helwingiaceae_to_aquifoliaceae))aquifoliales, ((escalloniaceae)escalloniales, (((rousseaceae, campanulaceae), pentaphragmataceae), (((argophyllaceae, phellinaceae), alseuosmiaceae)argophyllaceae_to_alseuosmiaceae, stylidiaceae, (menyanthaceae, goodeniaceae, (calyceraceae, (((barnadesia, huarpea), (dasyphyllum, ((chuquiraga, doniophyton), (schlechtendalia, (dasyphyllum_diacanthoides, (fulcaldea, arnaldoa))))))), (stifftia, (onoseris, (aphylloclados, plazia)), (((pachylaena, ((duidaea, (chaetanthera, mutisia)), (chaptalia, (leibnitzia, piloselloides, gerbera))))), ((leucheria, jungia), ((acourtia, proustia, trixis)), (adenocaulon, (perezia, (triptilion, nassauvia))))))), ((gochnatia, cnicothamnus), (hecastocleis, (((dicoma, pasaccardoa), (oldenburgia, (brachylaena, tarchonanthus), (cardopatiinae, ((atractylodes, (carlina, atractylis)), ((echinops, acantholepis), ((xeranthemum, chardinia), ((berardia, (onopordum, (synurus, alfredia))), (((ptilostemon, galactites), (cynara, ((picnomon, notobasis), (cirsium, silybum, (tyrimnus, carduus))))), (((outreya, jurinea), (cousinia, arctium)), (serratula, ((acroptilon, callicephalus), (zoegea, centaurea)))))))))), ((ainsliaea, (myripnois, pertya)), (gymnarrhena, ((((warionia, gundelia), ((scolymus, (tragopogon, scorzonera)), (((uropappus, microseris), (arnoseris, cichorium)), (((picris, leontodon), (hyoseris, sonchus)),

((urospermum, chondrilla), (youngia, (rhagadioulus, lapsana))))))), (((haplocarpha, (cymbonotus, (arctotis, arctotheca))), (eremothamnus, ((didelta, berkheya), (hirpicium, (gazania, gorteria))))), (((oligactis, (liabum, sinclairia)), (paranephelius, ((munnozia, chrysactinium), (erato, philoglossa)))), (distephanus, (((linzia, vernonia), ((vernonia2, baccharoides), (gymnanthemum, hesperomannia))), ((cabobanthus, (centrapalus, ((centauropsis, vernonia3), ((orbivestus, (vernonastrum, vernonia4)), (gutenbergia, (ethulia, (hilliardiella, muschleria)))))), (stokesia, (hololepis, (stramentopappus, (lepidonia, bolanosa))), ((chresta, (critoniopsis, (elephantopus, (lessingianthus, (chrysolaena, lepidaploa))))), ((albertinia, sipolisia), vernonanthura)))))))), (corymbium, ((blennosperma, ((gynoxys, gynoxys2), roldana, (tussilago, petasites), (ligularia, parasenecio), (othonna, euryops), (senicio_scaposa, senicio_medley-woodii), ((pericallis, (cineraria, dendrosenecio)), ((senicio_flaccidus, (senicio_costaricensis, (senicio_sphaerocephalus, senicio_serra))), (senicio_inornatus, senicio_subsessilis, senicio_ochrocarpus, (senicio_umbrusus, (senicio_vulgaris, (senicio_squalida, senicio_glauca)))), ((packera, (senicio_incanus, (senicio_paludosus, senicio_jacobea))), ((gynura, kleinia), (delairea, senicio_rowleyanus)))))))), ((((dimorphotheca, (osteospermum, calendula)), ((athrixia, (arrowsmithia, (rosenia, oedera))), (phaenocoma, (vellereophyton, ((stoebe, edmondia), ((gamochaetopsis, (plecostachys, antennaria, (tenrhynea, gamochaeta))), (jalcophila, (pterygopappus, (((anaxeton, (langebergia, petalacte)), (anaphalis, (pseudognaphalium, helicrhysum))), ((telfordia, (ozothamnus, cassinia)), ((apalochlamys, ammobium), ((myriocephalus, (leucophyta, craspedia)), (podolepis, (millotia, hyalosperma))))))))))))), ((amellus, (commidendron, ((chiliotrichum, olearia), (pteronia, (orithrophium, (conyza, ((remya, (olearia2, calotis)), ((grangea, olearia3), (vittadinia, brachyscome)), (lagenifera, (erigeron, (diplostephium, (podocoma, (solidago, (grindelia, (erigeron2, conyza2))))))))))))), (osmitopsis, (athanasia, (hippia, (schistostephium, (soliva, (lidbeckia, ((ursinia, eriocephalus), (((hymenolepis, ((cotula, cotula2), lasiospermum)), (leucanthemella, (seriphidium, (kaschgaria, artemisia)), (crossostephium, arctanthemum, (ajania, tripleurospermum)))))), ((oncosiphon, (cymbopappus, pentzia)), (microcephala, ((anthemis, tanacetum, matricaria, anacyclus, achillea, (gonospermum, lugoa)), ((leucanthemum, (rhodanthemum, glossopappus)), (lonas, ((chamaemelum, santolina), (aaronsohnia, (chrysanthemum, ismela))))))))))))))), (((zoutpansbergia, callilepis), ((inula, blumea), (pegolettia, (cratystylis, (epaltes, (streptoglossa, pluchea)))))), ((athroisma, blepharispermum), ((marshallia, pelucha, plateilema, (psathyrotes, trichoptilium), ((helenium, (balduina, gaillardia)), (psilostrophe, ((amblyolepis, tetraneuris), (baileya, hymenoxys))))), ((cosmos, (bidens, coreopsis)), ((neurolaena, (((coulterella, varilla), (jaumea, (flaveria, (haploesthes, sartwellia))), ((oxypappus, pseudoclappia), ((pectis, porophyllum), (nicolletia, ((tagetes, (adenophyllum, thymophylla)), (clappia, (arnicastrum, jamesianthus)))))))), ((chaenactis, dimeresia, orochaenactis), (loxothysanus, (((bartlettia, chamaechaenactis), (hymenopappus, thymopsis)), (((peucephyllum, psathyrotopsis), (espejoa, (chaetymenia, hypericophyllum))), (schkuhria, ((achyropappus, bahia), ((florestina, palafoxia), (platyschkuhria, (amauriopsis, hymenothrix))))))))))), (polymnia, ((wyethia, (chromolepis, (ambrosia, (helianthus, (rudbeckia, trichocoryne))))), ((galinsoga, melampodium, smallanthus), (((eutetras, (amauria, (pericome, perityle))), (hofmeisteria, (ageratina, ((carminatia, (brickellia, kuhnia)), ((fleischmannia, (ageratum, conoclinium)), (steviopsis, ((eupatoriadelphus, eupatorium, liatris), ((chromolaena, praxelis), (stomatanthes, (trichogonia, (acritopappus, campuloclinium))))))))))), ((monolopia, (lasthenia, (amblyopappus, baeriopsis))), (constancea, syntrichopappus, (eriophyllum, pseudobahia)), (venegasia, (eatonella, hulsea), (arnica, (achyrachaena, adenothamnus, blepharipappus, calycadenia, holocarpha, lagophylla, raillardella, (blepharizonia, hemizonia), (holozonia, layia), ((hemizonella, kyhosia), (anisocarpus, (carlquistia, madia), (argyroxiphium, dubauta, wilkesia)))))))))))))))))))))))))))) asteraceae))))) asterales, ((((adoxaceae, caprifoliaceae) dipsacales, (paracryphiaceae) paracryphiales), (pennantiaceae, (torricelliaceae, (griseliniaceae, (pittosporaceae, (araliaceae, (myodocarpaceae, apiaceae))))))apiales), (bruniaceae, columelliaceae) bruniales))) campanulids) lamiids_to_campanulids) ericales_to_asterales) asterids))) subasterids) pentapetalids) core_eudicots) trochodendrales_to_asterales) sabiales_to_asterales) eudicots) ceratophyllales_and_eudicots) poales_to_asterales) magnoliales_to_asterales) austrobaileyales_to_asterales) nymphaeales_to_asterales) angiosperms) seedplants) euphyllophyte;

Supplementary Table 2.2

Node ages that were used for the age calibration of the phylogeny for the phylodiversity analysis. All age estimates were extracted from the age file 'age_exp' (Markus Gastauer, personal communication) which uses age estimates from Bell et al. (2010).

Node	Age [myr]
Acanthaceae	38
Achariaceae	79
Adoxaceae	31
Akaniaceae	6
Alismatales	107
Altingiaceae	7
Amaranthaceae	37
Amaranthaceae to Caryophyllaceae	55
Amaryllidaceae	30
Angiosperms	147
Annonaceae	23
Apiaceae	29
Apiales	49
Apocynaceae	21
Aquifoliales	88
Araceae	79
Araliaceae	18
Araucariaceae to Podocarpaceae	257
Arecaceae	31
Argophyllaceae to Alseuosmiaceae	49
Aristolochiaceae	91
Asparagaceae	42
Asparagales	92
Aspleniaceae to Onocleaceae	95
Asteraceae	40
Asterales	77
Asterids	104
Austrobaileyales	89
Austrobaileyales to Asterales	144
Berberidaceae	33
Betulaceae	18
Bignoniaceae	25
Boraginaceae	54
Brassicaceae	31
Brassicaceae to Cleomaceae	41
Brassicales	83
Bromeliaceae	20
Bursa to Anaca	50
Buxaceae	98
Cactaceae to Portulaceae	21
Calycanthaceae	98
Campanulaceae	53
Campanulids	93
Canellaceae	10
Canellales	77
Cannabaceae	36
Cannabaceae to Moraceae	54
Caprifoliaceae	36
Caryophyllales	99
Celastraceae	53
Celastrales	71
Celastrales to Malpighiales	101
Ceratophyllales and Eudicots	129
Chloranthaceae	121
Chrysobalanaceae	16
Circaeasteraceae	45
Combretaceae	21
Commelinales	70
Commelinids	96
Convallariaceae	19
Convolvulaceae	24
Core eudicots	117

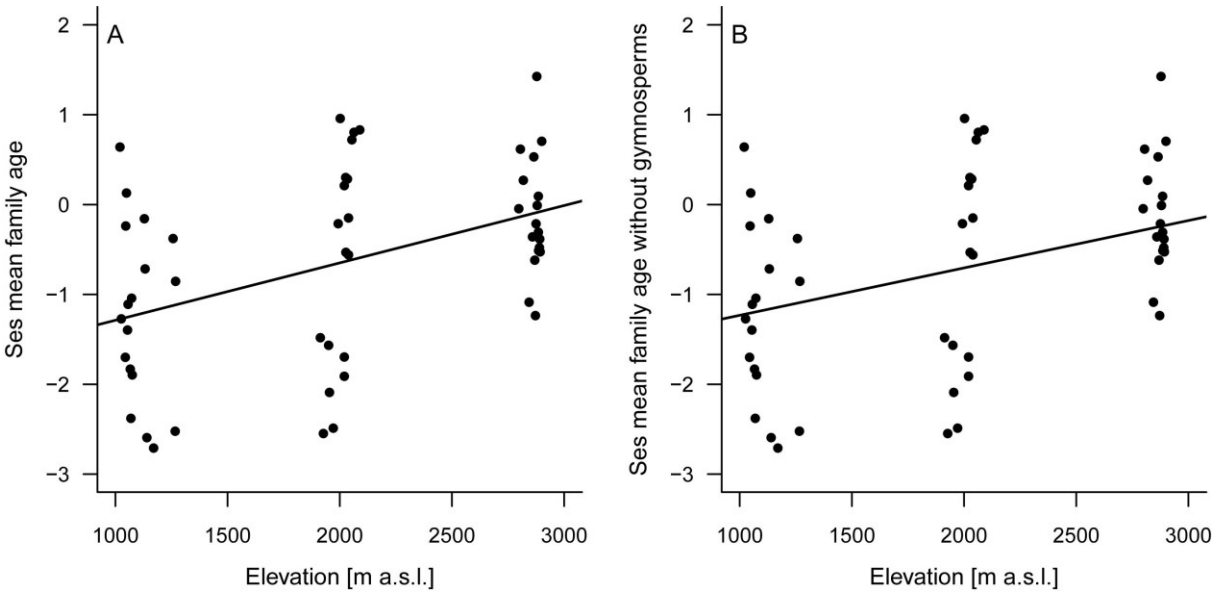
Strelitziaceae	23	Taxaceae to Cupressaceae	227	Verbenaceae	29
Strelitziaceae to Lowiaceae	40	Tecophilaeaceae	45	Vitaceae	65
Stylidiaceae	65	Ternstroemiaceae	51	Winteraceae	18
Styracaceae	36	Thymelaeaceae	36	Zingiberaceae	18
Styracaceae to Diapensiaceae	51	Tofieldiaceae	61	Zingiberales	84
Subasterids	116.8	Trochodendraceae	19		
Subrosid	116.8	Urticaceae	34		

Supplementary Table 2.3

Family ages that were used for the analysis of family ages of the tree assemblages. All family age estimates were extracted directly from the phylogeny provided by Davies et al. (2004) which is available online (http://biology.mcgill.ca/faculty/davies/Data/Dated tree Ultrametric.phy, accessed 11/2015).

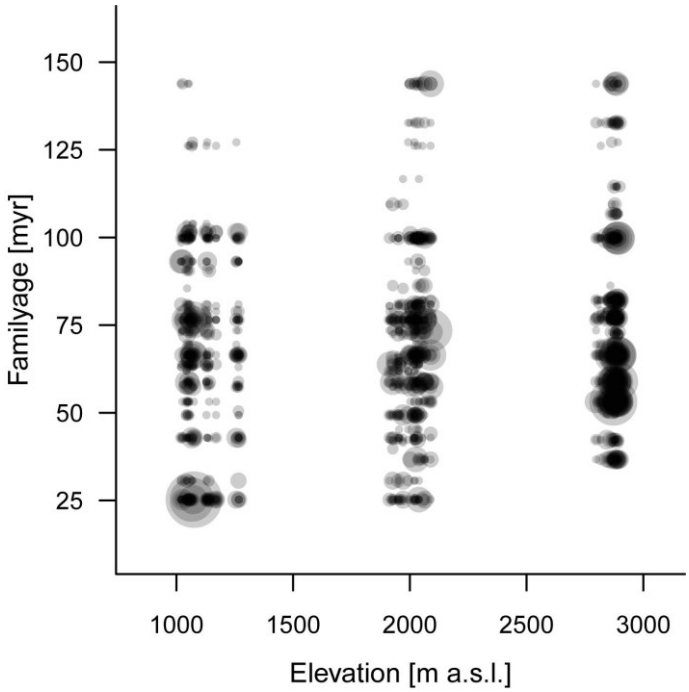
Family	Age [myr]	Ericaceae	76.805507	Picramniaceae	103.862183
Actinidiaceae	64.655587	Euphorbiaceae	57.379803	Piperaceae	80.450584
Adoxaceae	86.272046	Fabaceae	63.803841	Podocarpaceae	NA
Alzateaceae	58.2997	Hernandiaceae	116.66751	Polygalaceae	72.281677
Anacardiaceae	42.881471	Hypericaceae	44.060641	Polygonaceae	59.246611
Annonaceae	78.890161	Icacinaceae	98.569468	Primulaceae	36.689299
Apocynaceae	67.046339	Lacistemataceae	58.039526	Proteaceae	126.136464
Aquifoliaceae	77.025746	Lamiaceae	39.728399	Rhizophoraceae	76.370622
Araliaceae	69.439409	Lauraceae	99.807051	Rosaceae	72.977131
Asteraceae	42.307411	Lecythidaceae	90.558439	Rubiaceae	76.504911
Bignoniaceae	45.247531	Malpighiaceae	73.492593	Rutaceae	53.366445
Boraginaceae	85.473059	Malvaceae	65.834252	Sabiaceae	127.156694
Brassicaceae	50.503186	Melastomataceae	66.475919	Salicaceae	58.039526
Brunelliaceae	49.651267	Meliaceae	49.350353	Sapindaceae	58.745333
Burseraceae	42.881471	Monimiaceae	99.807051	Sapotaceae	93.138822
Cannabaceae	41.479856	Moraceae	25.229981	Siparunaceae	109.456993
Caryophyllales b	30.642085	Myricaceae	51.00971	Solanaceae	61.877995
Celastraceae	41.983088	Myristicaceae	101.535374	Staphyleaceae	42.744786
Chloranthaceae	143.833806	Myrtaceae	80.913749	Styracaceae	60.783984
Chrysobalanaceae	63.027391	Olacaceae	114.500865	Symplocaceae	82.167251
Clethraceae	78.134138	Santalaceae	114.500865	Theaceae	82.167251
Clusiaceae	58.922056	Loranthaceae	114.500865	Thymelaeaceae	72.421904
Combretaceae	74.034094	Palmae	100.975677	Urticaceae	25.229981
Cunoniaceae	53.150235	Pentaphylacaceae	79.141798	Violaceae	58.675148
Elaeocarpaceae	53.150235	Phyllanthaceae	73.492593	Winteraceae	106.76463

Supplementary Figure 2.1



Standardized effect sizes (ses) of the mean family ages of the tree assemblages (A) and of assemblages after removing gymnosperms (B) in relation to elevation. We observed significant positive relationships between for the complete tree assemblage (A) and after excluding gymnosperms from the dataset (B). Lines indicate significant linear relationship ($p < 0.05$).

Supplementary Figure 2.2



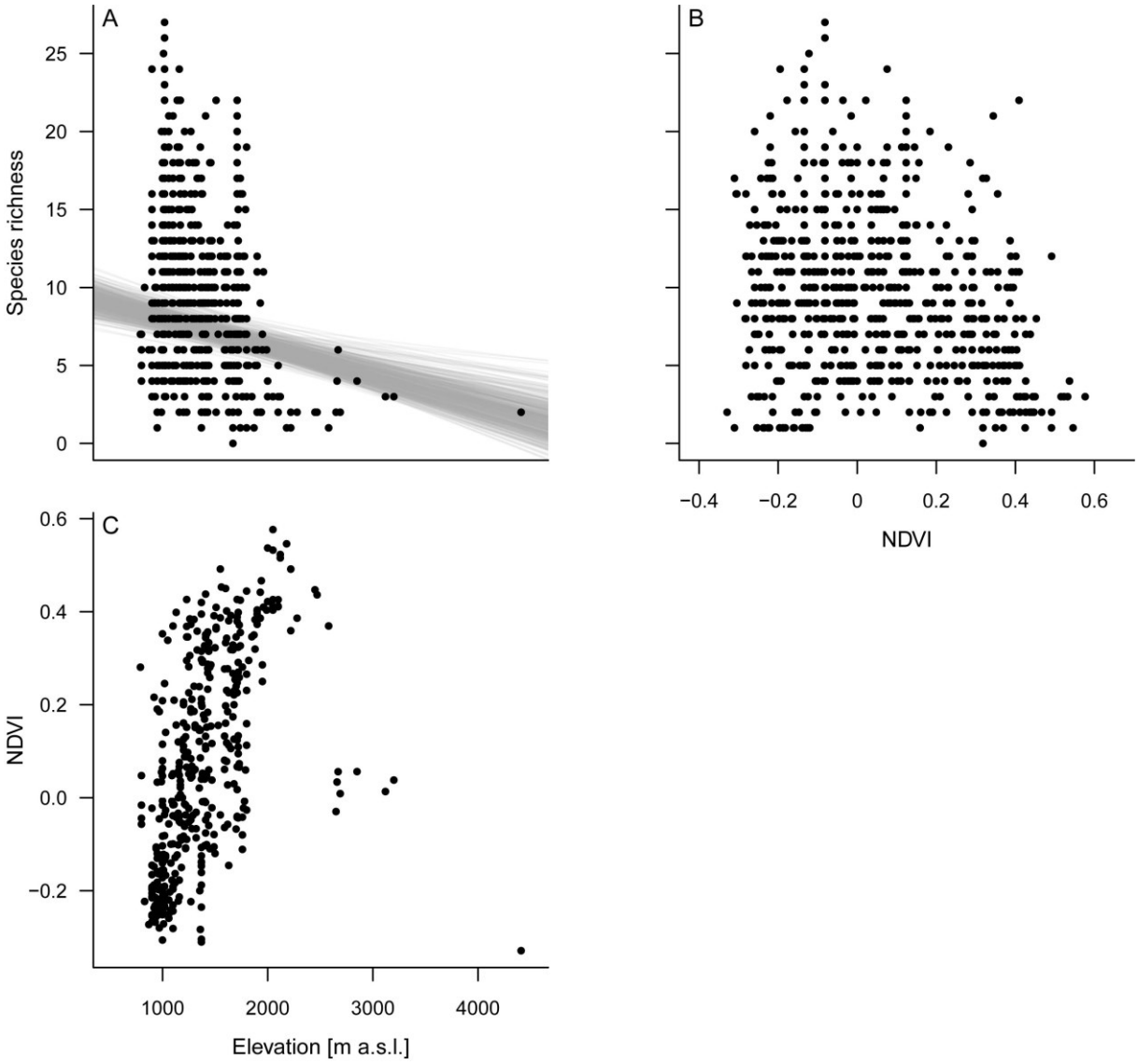
Family age of observed tree species in relation to elevation. Each circle represents one species at its observed elevation. The radius of the circles is proportional to the number of individuals.

Chapter 9

Appendix chapter 3

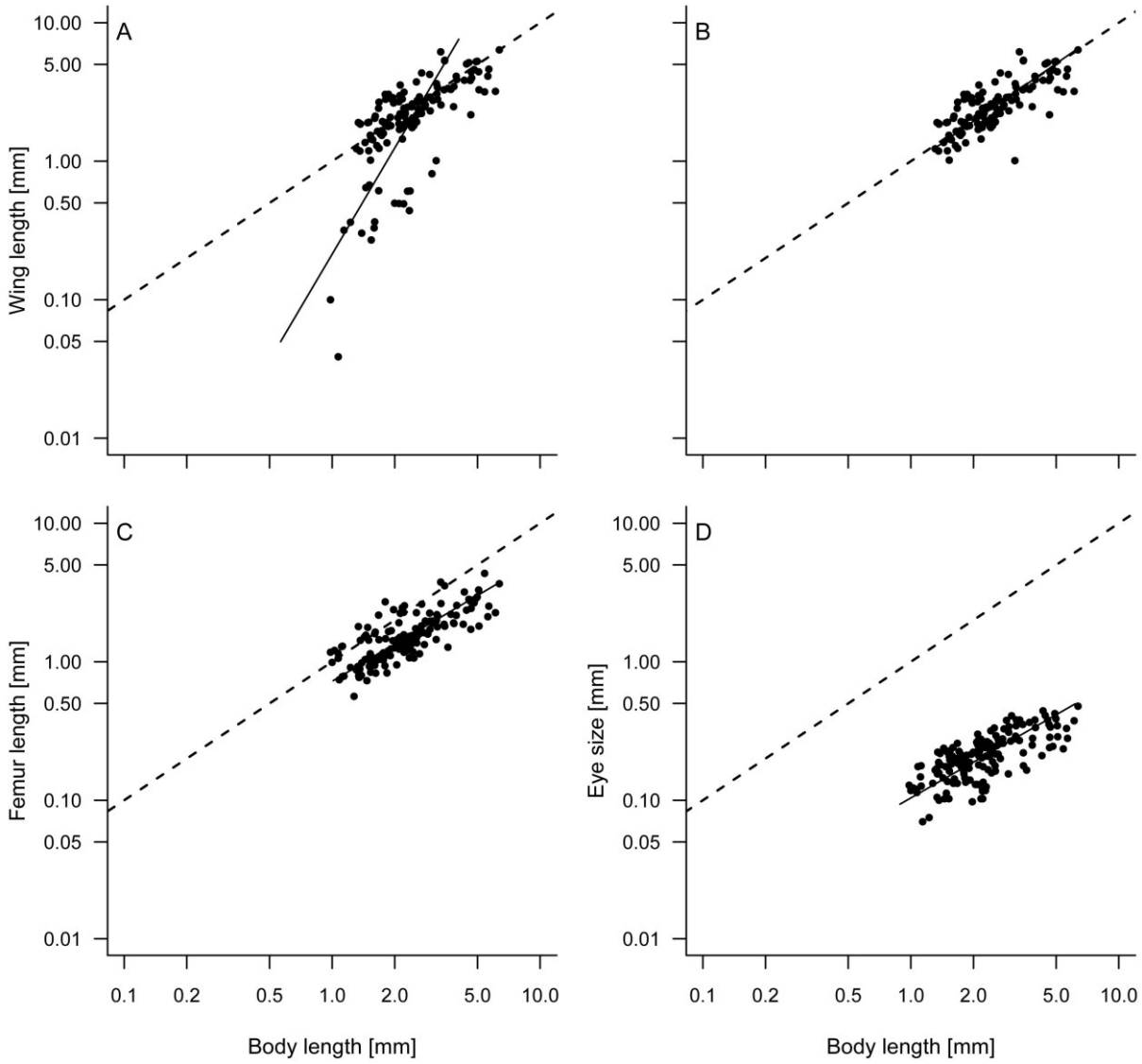
Beyond body size:
Consistent decrease of traits within orthopteran assemblages with elevation

Supplementary Figure 3.1



Patterns of species richness with increasing elevation (A) and with increasing normalized difference vegetation index (NDVI) (B), and pattern of NDVI along the elevation gradient (C). Models were fitted following the approach described in the Methods section of the manuscript using Poisson error distribution. Lines show fitted values for significant relationships, where each line represents one posterior sample mean from generalized linear mixed effect models. Dots depict underlying raw data from 440 study plots.

Supplementary Figure 3.2



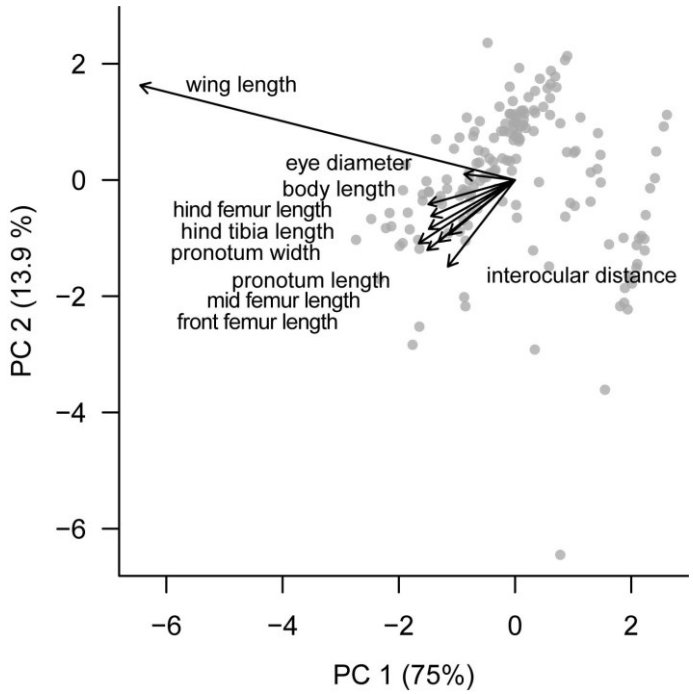
Allometric relationships between the three morphological traits wing length (A, B), hind femur length (C), and eye size (D) of 160 orthopteran species. Shown are original trait values. The solid lines represent slopes of major axis regression; the dashed lines indicate isometry. All axes were $\log_{10}$-tranformed. Species with a wing length of zero were excluded from the analysis in A; species with a wing length < 1 mm were excluded from the analysis in B. For regression statistics, see Supplementary Table 3.1.

Supplementary Table 3.1

Allometric relationships between body length and each of the three morphological traits wing length, hind femur length, and eye size of 160 orthopteran species. Log_{10}-transformed data are shown. Slopes (b) significantly differing from 1 are in bold. Species with wing length of zero were excluded from analysis A. Species with wing length < 1 mm were excluded from analysis B. r: sample correlation between residuals and fitted values; CI: confidence interval of slope; P: P-value.

				F	r	*b*	CI 95%		P
A	Wing length	~	body length	124	0.69	**2.6**	2.1	3.1	0
B	Wing length	~	body length	0.36	0.055	1.1	0.90	1.2	0.55
C	Hind femur length	~	body length	3.25	−0.14	0.89	0.78	1.0	0.073
D	Eye size	~	body length	3.5	−0.15	0.86	0.73	1.0	0.063

Supplementary Figure 3.3



Principal component analysis of orthopteran species and ten morphological traits. The biplot represents covariation among body length; wing length; length of front, middle, and hind femur; length of hind tibia; eye diameter; interocular distance; pronotum width; and pronotum length. The length of the arrows indicates the degree of variation in a component, i.e., relatively longer lines indicate relatively higher variation. Lines pointing in the same direction indicate a positive correlation between components; perpendicular lines indicate no relationship. The first principal component (PC 1) explains 75% of the variance, and the second principal component (PC 2) accounts for 14% of the variance. We extracted the species scores and multiplied the scores by −1 as a measure of the body size of species.

Supplementary Table 3.2

Ranges of original trait values (MinO, MaxO), ranges of relative trait values (residuals from linear models of trait values plotted against body length; MinR, MaxR), means and standard deviations (SD).

	Min_O	Max_O	$Mean_O$	SD_O	Min_R	Max_R	SD_R
Body length	0.98	6.4	2.4	1.2			
Wing length	0.0	6.4	2.0	1.5	-3.8	3.3	0.99
Hind femur length	0.56	4.4	1.6	0.67	-0.95	1.8	0.44
Eye size	0.070	0.48	0.22	0.083	-0.14	0.15	0.058

Supplementary Table 3.3

Explained variance and loadings of the first four principal components of orthopteran species and ten morphological traits.

	PC 1	PC 2	PC 3	PC 4
Explained variance [%]	75	14	5.2	2.8
Body length	−0.195	−0.127	0.411	−0.080
Pronotum length	−0.173	−0.324	0.348	0.105
Pronotum width	−0.149	−0.286	0.299	0.149
Eye diameter	−0.115	0.030	0.657	−0.0865
Interocular distance	−0.152	−0.453	−0.192	0.721
Wing length	−0.845	0.495	−0.123	0.137
Hind femur length	−0.189	−0.189	0.00152	−0.360
Hind tibia length	−0.194	−0.256	−0.147	−0.445
Middle femur length	−0.217	−0.331	−0.237	−0.189
Front femur length	−0.198	−0.367	−0.242	−0.227

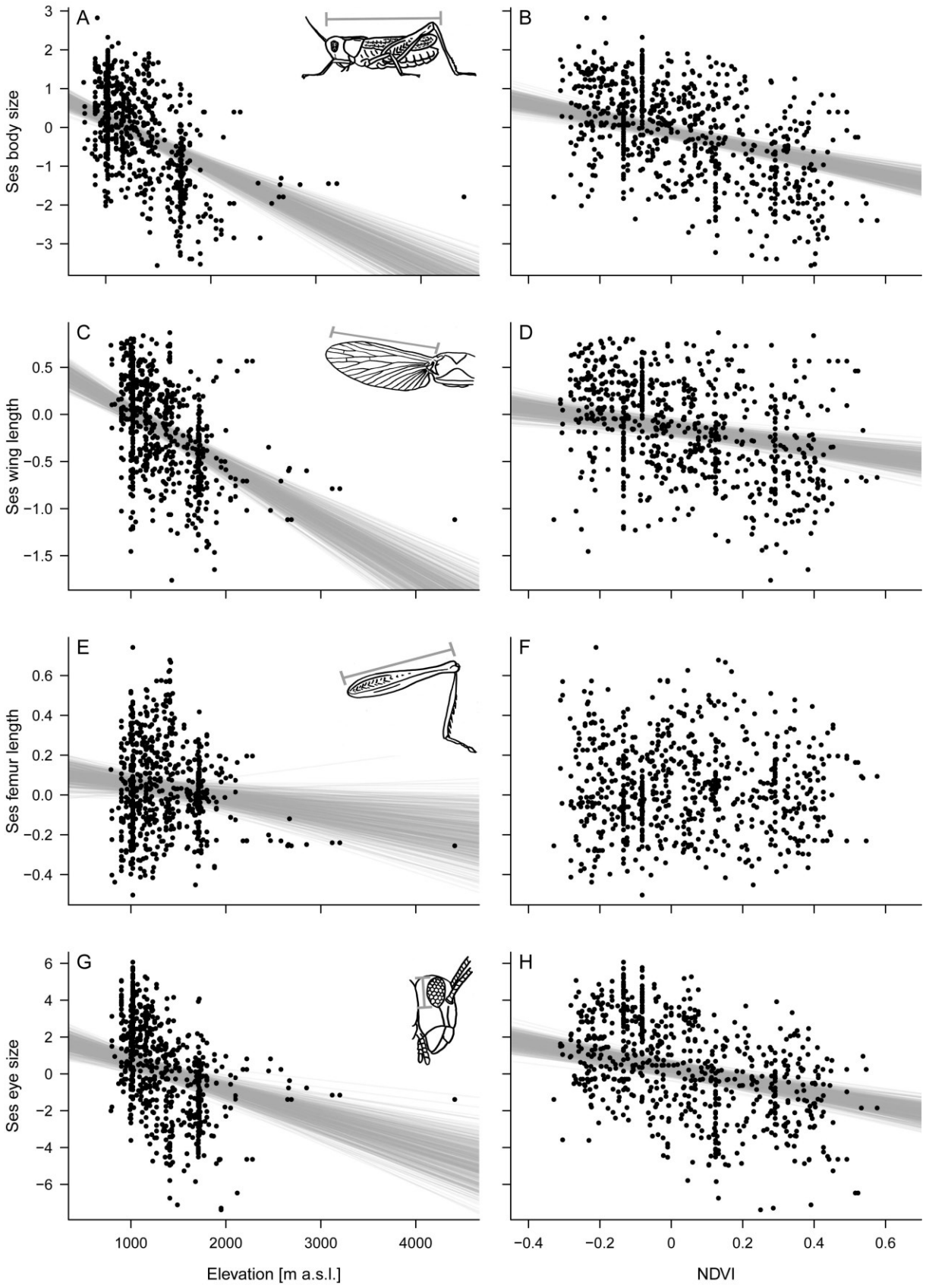
Supplementary Table 3.4

Posterior estimates of species richness of orthopteran assemblages with elevation and normalized difference vegetation index (NDVI) derived from Bayesian linear mixed models.

Parameter	Mean	SD	CI 2.5%	CI 97.5%
Intercept	**2.0**	0.062	1.9	2.1
Elevation	**−0.13**	0.034	−0.20	−0.067
NDVI	−0.035	0.031	−0.094	0.027

Notes: Study plots and month of sampling nested in sampling year were included as random effects in all models. Predictors were standardized to zero mean and unit variance to ease the comparison of effect sizes. Model was fitted using Poisson error distribution. Mean: mean slope of the predictor; SD: standard deviation; CI: credible interval; intercept: species richness at mean elevation and mean NDVI. Boldface indicates posterior estimates of the predictors with significant effects on species richness (CI does not include zero).

Supplementary Figure 3.4



Patterns of community weighted mean values of standardized effect sizes (ses) of body size (A, B), wing length (C, D), hind femur length (E, F), and eye size (G, H) with increasing elevation (A, C, E, G), and increasing normalized difference vegetation index (NDVI) (B, D, F, H). Body size was calculated as the species score from a

multidimensional analysis of nine orthopteran traits (for details, see Methods section). Trait values are measures relative to body length, calculated as the residues of a linear model of the trait values plotted against body length. For calculation of standardized effect sizes, see the Methods section. Lines are shown for significant relationships, where each line represents one posterior sample mean. Dots depict underlying raw data from 440 study plot.

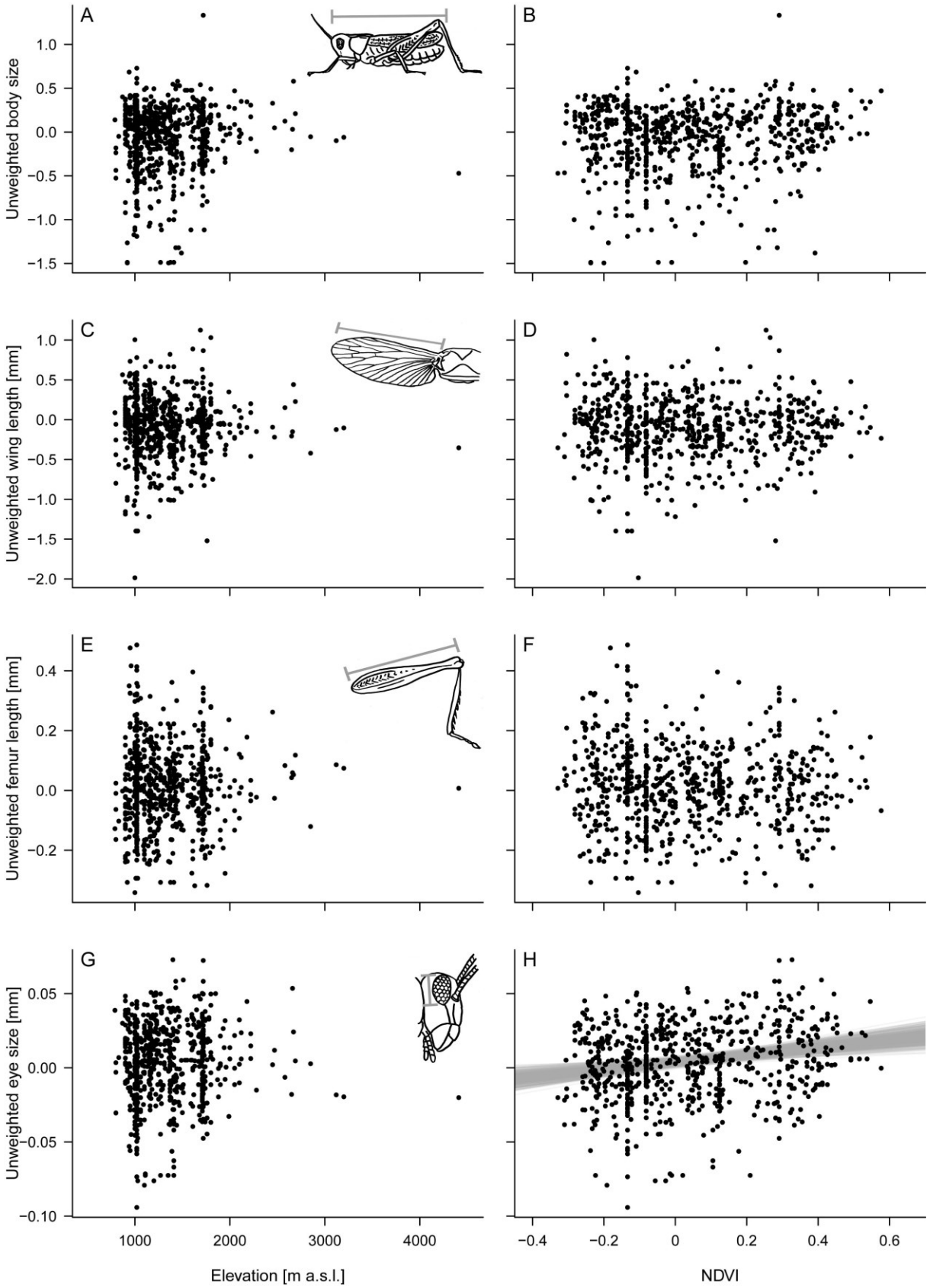
Supplementary Table 3.5

Posterior estimates of the community weighted mean (CWM) values of standardized effect sizes (ses) of body size (ses model 1), wing length (ses model 2), hind femur length (ses model 3), and eye size (ses model 4) with elevation and normalized difference vegetation index (NDVI) derived from Bayesian linear mixed models.

Parameter	Mean	SD	CI 2.5%	CI 97.5%
Ses model 1: CWM of ses body size				
Intercept	**−0.19**	0.071	−0.33	−0.045
Elevation	**−0.47**	0.050	−0.57	−0.38
NDVI	**−0.38**	0.047	−0.47	−0.29
Ses model 2: CWM of ses wing length				
Intercept	**−0.16**	0.041	−0.25	−0.088
Elevation	**−0.22**	0.022	−0.26	−0.18
NDVI	**−0.10**	0.021	−0.15	−0.062
Ses model 3: CWM of ses hind femur length				
Intercept	0.035	0.022	−0.0070	0.079
Elevation	**−0.027**	0.011	−0.048	−0.0049
NDVI	0.0016	0.011	−0.019	0.022
Ses model 4: CWM of ses eye diameter				
Intercept	0.18	0.21	−0.24	0.57
Elevation	**−0.57**	0.10	−0.77	−0.37
NDVI	**−0.71**	0.10	−0.91	−0.51

Notes: Study plots and month of sampling nested in sampling year were included as random effects in all models. Predictors were standardized to zero mean and unit variance to ease the comparison of effect sizes. Body size was calculated as the species score from a multidimensional analysis of nine orthopteran traits (for details, see Methods section). Trait values for the CWM calculation used in models 2, 3, and 4 were residuals of linear regressions of the trait values plotted against body length. For details on the calculation of ses, see Methods section. Models were fitted using normal error distribution. Mean: mean slope of the predictor; SD: standard deviation; CI: credible interval; intercept: response value at mean elevation and mean NDVI. Boldface indicates posterior estimates of predictor variables with significant effects on the model response (CI does not include zero).

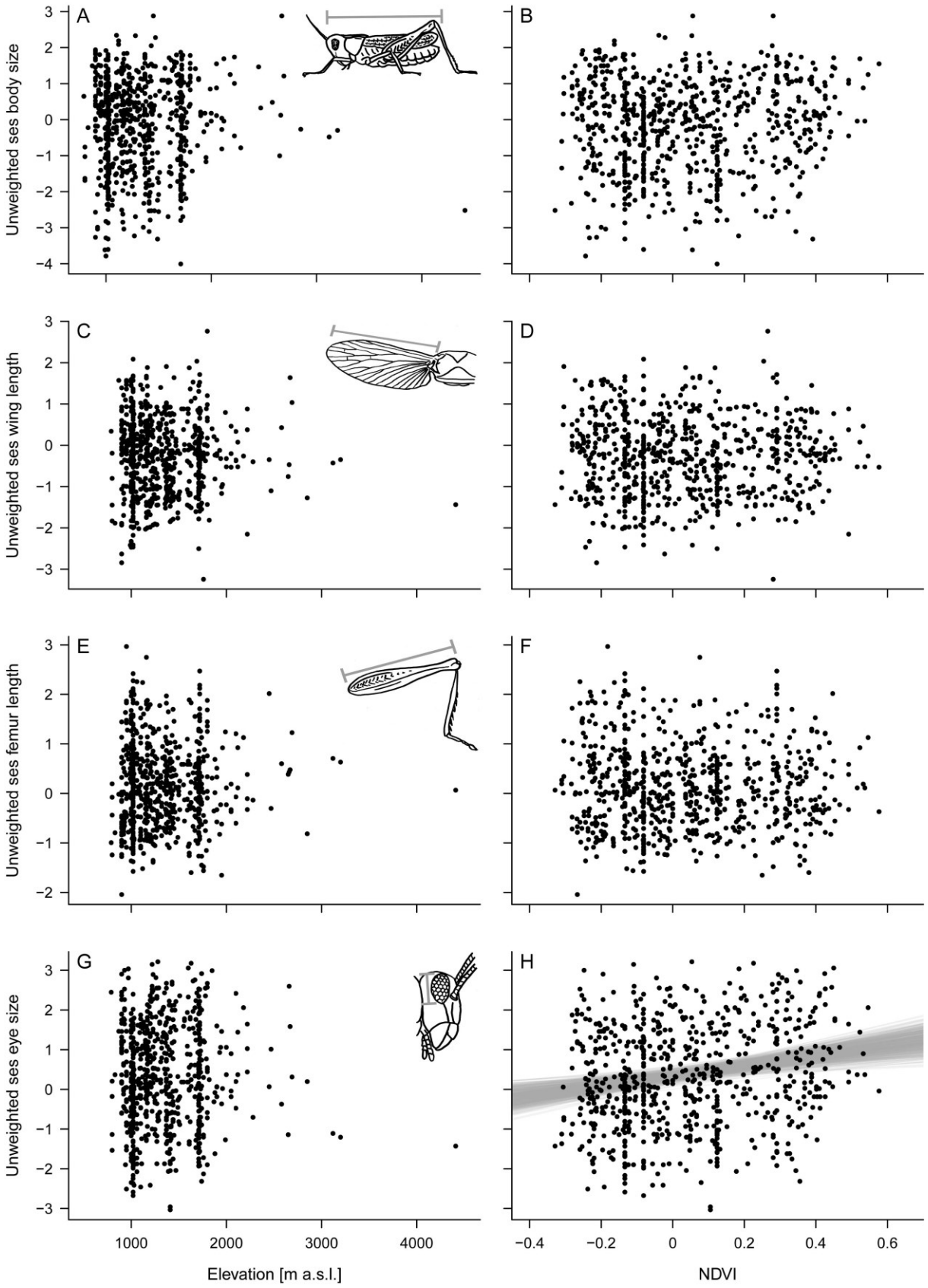
Supplementary Figure 3.5



Patterns of unweighted community mean values of body size (A, B), wing length (C, D), hind femur length (E, F), and eye size (G, H) with increasing elevation (A, C, E, G), and increasing normalized difference vegetation index (NDVI) (B, D, F, H). Body size was calculated as the species score from a multidimensional analysis of nine

orthopteran traits (for details, see Methods section). Trait values are measures relative to body length, calculated as the residues of a linear model of the trait values plotted against body length. Lines are shown for significant relationships, where each line represents one posterior sample mean. Dots depict underlying raw data from 440 study plots.

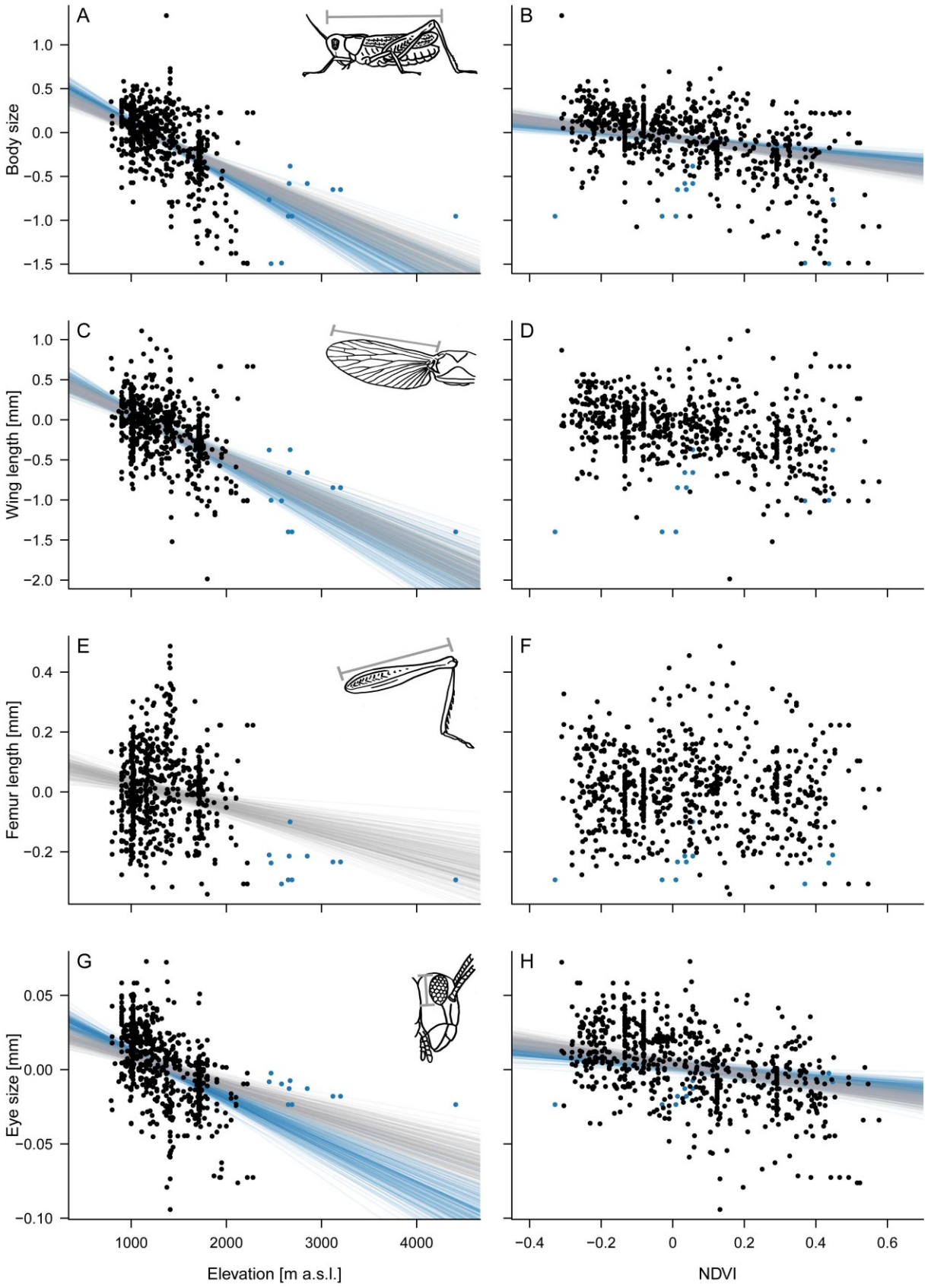
Supplementary Figure 3.6



Patterns of community weighted mean values of standardized effect sizes (ses) of unweighted body size (A, B), wing length (C, D), hind femur length (E, F), and eye size (G, H) with increasing elevation (A, C, E, G), and increasing normalized difference vegetation index (NDVI) (B, D, F, H). Body size was calculated as the species

score from a multidimensional analysis of nine orthopteran traits (for details, see Methods section). Trait values are measures relative to body length, calculated as the residues of a linear model of the trait values plotted against body length. For calculation of ses, refer to the Methods section. Lines are shown for significant relationships, where each line represents one posterior sample mean. Dots depict underlying raw data from 440 study plots.

Supplementary Figure 3.7



Patterns of community weighted mean values of body size (A, B), wing length (C, D), hind femur length (E, F), and eye size (G, H) with increasing elevation (A, C, E, G), and increasing normalized difference vegetation index (NDVI) (B, D, F, H). Body size was calculated as the species score from a multidimensional analysis of nine

orthopteran traits (for details, see Methods section). Trait values are measures relative to body length, calculated as the residues of a linear model of the trait values against body length. We reanalyzed the relationships for a reduced dataset, where we excluded high elevation plots (> 2300 m a.s.l.; blue dots). Dots depict underlying raw data from 440 study plots. Lines represent one posterior sample mean for significant relationships, both for the complete dataset (gray lines) and for the reduced dataset (blue lines). Note that the significant relationship between hind femur length and elevation is not significant when we excluded plots higher than 2300 m a.s.l. from the dataset.

Supplementary Table 3.6

Posterior estimates of the community weighted means (CWM) of body size (reduced (red) model 1), wing length (red model 2), hind femur length (red model 3), and eye size (red model 4) with elevation and normalized difference vegetation index (NDVI) derived from Bayesian linear mixed models when using a reduced data set.

Parameter	Mean	SD	CI 2.5%	CI 97.5%
Red model 1: CWM of body size				
Intercept	**−0.085**	0.021	−0.12	−0.044
Elevation	**−0.21**	0.023	−0.25	−0.16
NDVI	**−0.089**	0.018	−0.12	−0.052
Red model 2: CWM of wing length				
Intercept	**−0.11**	0.029	−0.17	−0.055
Elevation	**−0.22**	0.027	−0.27	−0.17
NDVI	−0.022	0.021	−0.062	0.019
Red model 3: CWM of hind femur length				
Intercept	0.010	0.012	−0.012	0.035
Elevation	−0.0064	0.0097	−0.025	0.012
NDVI	−0.0066	0.0075	−0.021	0.0082
Red model 4: CWM of eye size				
Intercept	0.0019	0.0019	−0.0020	0.0054
Elevation	**−0.011**	0.0015	−0.014	−0.0081
NDVI	**−0.0051**	0.0012	−0.0075	−0.0029

Notes: The data set excluded all study plots at elevations > 2300 m a.s.l., where sampling intensity was low, resulting in 723 included observations from 429 plots. Study plots and month of sampling nested in sampling year were included as random effects in all models. Predictors were standardized to zero mean and unit variance to ease the comparison of effect sizes. Trait values for the CWM calculation used in models 2, 3, and 4 were residuals of linear regressions of the trait values plotted against body length. Models were fitted using normal error distribution. Mean: mean slope of the predictor; SD: standard deviation; CI: credible interval; intercept: response value at mean elevation and mean NDVI. Boldface indicates posterior estimates of predictor variables with significant effects on the model response (CI does not include zero).

Chapter 10

Appendix chapter 4

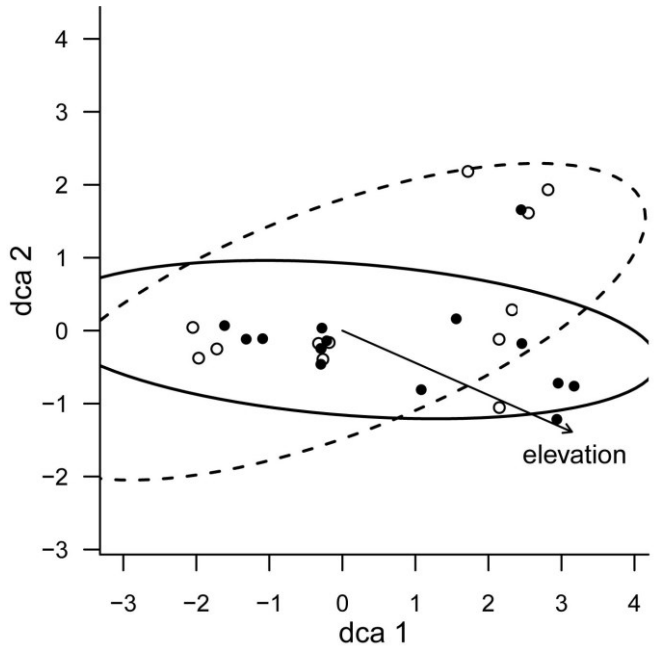
Ants as indicators of environmental change and ecosystem processes

Supplementary Table 4.1

Changes in ant species richness (model 1), (raw) functional richness of ant assemblages (model 2), and predation of artificial caterpillars (model 3) with elevation, drier vs. wetter season, and forest degradation. Linear mixed effect models were used for models 1, and 2, and a generalized linear mixed effect model was used for model 3. Study plots were included as random effect in models 1–3 to correct for pseudoreplication; model 3 included each observation as a random effect to remove overdispersion. Boldface indicates significant values.

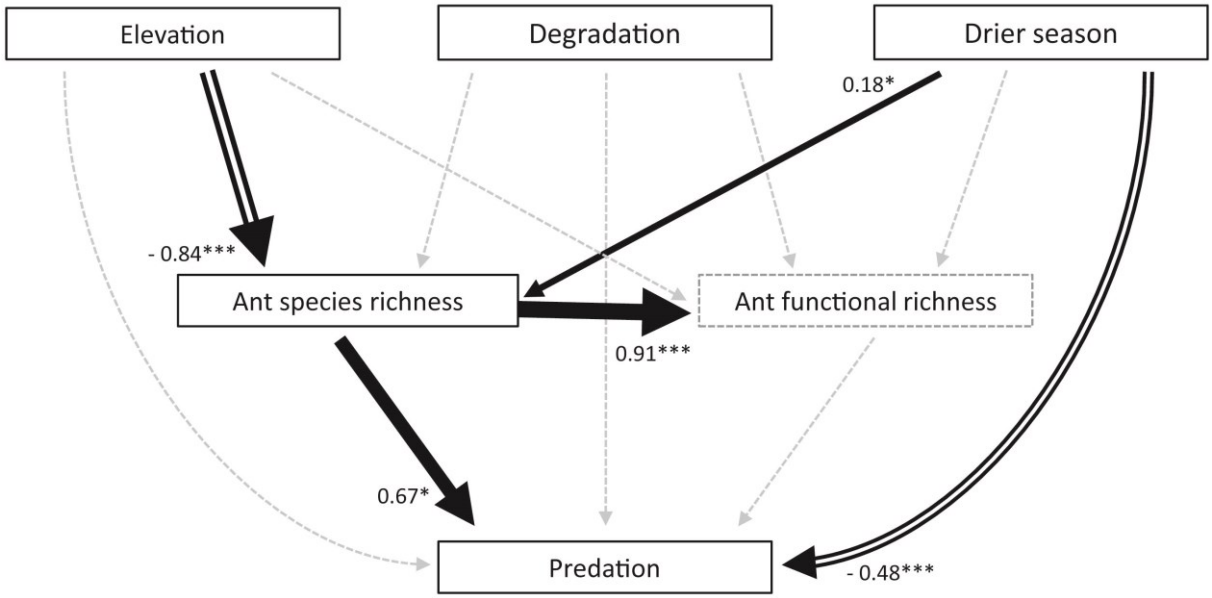
Source of variation	Estimate	*z-value*	*p-value*
Model 1: Ant species richness			
Elevation	$-8.4 * 10^{-1}$	−10.7	< **0.001**
Season	$1.8 * 10^{-1}$	2.5	< **0.1**
Degradation	$2.1 * 10^{-2}$	0.27	0.78
Model 2: Functional richness			
Elevation	$3.8 * 10^{-2}$	0.25	0.80
Season	$6.5 * 10^{-2}$	0.85	0.40
Degradation	$-6.0 * 10^{-2}$	−0.74	0.46
Ant species richness	$9.1 * 10^{-1}$	6.5	< **0.001**
Model 3: Predation of artificial caterpillars			
Elevation	$1.7 * 10^{-2}$	0.068	0.95
Season	$-4.8 * 10^{-1}$	−3.4	< **0.001**
Degradation	$9.1 * 10^{-2}$	0.68	0.50
Ant species richness	$6.7 * 10^{-1}$	2.0	< **0.1**
Functional richness	$6.1 * 10^{-4}$	−0.002	1.0

Supplementary Figure 4.1



Changes of ant species composition in relation to elevation and forest degradation. Shown are the results of the site scores of a detrended correspondence analysis (decorana; triangles, natural forest plots; crosses, degraded forest plots) and the fitted environmental variables elevation (arrow) and forest degradation [centroids represent 95% interval for natural plots (solid line) and degraded plots (dotted line)]. The decorana (DCA) axes scale is in units of species standard deviations, which is a measure of beta-diversity. Elevation was strongly and positively correlated with the first axis (DCA 1; $r^2 = 0.92$, $p < 0.001$; Pearson product-moment correlation coefficients), but not with forest degradation ($r^2 = 0.0089$, $p = 0.72$; Pearson product-moment correlation coefficients).

Supplementary Figure 4.2



Path model for relationships between elevation (a proxy for temperature), season, forest degradation, species richness, and functional richness of ants, and predation of artificial caterpillars. The thickness of the solid arrows depict the values of the estimated effect sizes next to arrows; values in black and solid arrows indicate significant positive effects, framed arrows indicate significant negative effects with asterisks demarking the significance level ($0.050 < ^{*} > 0.010 < ^{**} > 0.001 < ^{***} > 0.000$). Note that ant functional richness does not differ for ant assemblages with randomly distributed sets of traits across species (indicated by dashed frame; cf. Figure 1B; for details, see Methods and Results section).

References

Abrams, P. A., O. Leimar, S. Nylin, and C. Wiklund. 1996. The effect of flexible growth rates on optimal sizes and development times in a seasonal environment. The American Naturalist 147:381–395.

Acharya, B. K., B. Chettri, and L. Vijayan. 2011. Distribution pattern of trees along an elevation gradient of Eastern Himalaya, India. Acta Oecologica 37:329–336.

Akin, S., and K. O. Winemiller. 2008. Body size and trophic position in a temperate estuarine food web. Acta Oecologica 33:144–153.

Alexander, G. 1951. The occurrence of Orthoptera at high altitudes, with special reference to Colorado Arcididae. Ecology 32:104–112.

Algar, A. C., J. T. Kerr, and D. J. Currie. 2009. Evolutionary constraints on regional faunas: whom, but not how many. Ecology Letters 12:57–65.

Allen, A., J. Gillooly, and J. Brown. 2007. Recasting the species-energy hypothesis: the different roles of kinetic and potential energy in regulating biodiversity. Scaling biodiversity:1–29.

Allen, A. P., J. H. Brown, and J. F. Gillooly. 2002. Global Biodiversity, Biochemical Kinetics, and the Energetic-Equivalence Rule. Science 297.

Allen, A. P., J. H. Brown, and J. F. Gillooly. 2003. Response to comment on "Global biodiversity, biochemical kinetics, and the energetic-equivalence rule." Science 299:346.

Andersen, A. N. 1986. Diversity, seasonality and community organization of ants at adjacent heath and woodland sites in Southeastern Australia. Australian Journal of Zoology 34:53–64.

Andersen, A. N. 1997. Functional groups and patterns of organization in North American ant communities: a comparison with Australia. Journal of Biogeography 24:433–460.

Andersen, A. N., and J. D. Majer. 2004. Ants show the way Down Under: invertebrates as bioindicators in land management. Frontiers in Ecology and the Environment 2:291–298.

Angilletta, M. J., T. D. Steury, and M. W. Sears. 2004. Temperature, growth rate, and body size in ectotherms: fitting pieces of a life-history puzzle. Integrative and comparative biology 44:498–509.

Antonelli, A., J. A. A. Nylander, C. Persson, and I. Sanmartín. 2009. Tracing the impact of the Andean uplift on Neotropical plant evolution. Proceedings of the National Academy of Sciences of the United States of America 106:9749–9754.

Arnan, X., X. Cerdá, and J. Retana. 2017. Relationships among taxonomic, functional, and phylogenetic ant diversity across the biogeographic regions of Europe. Ecography 40:448–457.

Asner, G. P., S. R. Loarie, and U. Heyder. 2010. Combined effects of climate and land-use change on the future of humid tropical forests. Conservation Letters 3:395–403.

Atkinson, D. 1994. Temperature and organism size—a biological law for ectotherms? Pages 1–58*in* M. Begon and A. H. Fitter, editors.Advances in Ecological Research. Academic Press, London.

Barnes, A. D., P. Weigelt, M. Jochum, D. Ott, D. Hodapp, N. F. Haneda, and U. Brose. 2016. Species richness and biomass explain spatial turnover in ecosystem functioning across tropical and temperate ecosystems. Philosophical Transactions of the Royal Society B: Biological Sciences 371:20150279.

Bartholomew, G. A., J. R. B. Lighton, and D. H. J. Feener. 1988. Energetics of trail running, load carriage, and emigration in the column-raiding army ant *Eciton hamatum*. Physiological Zoology 61:57–68.

Basset, Y., L. Cizek, P. Cuenoud, R. K. Didham, F. Guilhaumon, O. Missa, V. Novotny, F. Odegaard, T. Roslin, J. Schmidl, A. K. Tishechkin, N. N. Winchester, D. W. Roubik, H.-P. Aberlenc, J. Bail, H. Barrios, J. R. Bridle, G. Castano-Meneses, B. Corbara, G. Curletti, W. Duarte da Rocha, D. De Bakker, J. H. C. Delabie, A. Dejean, L. L. Fagan, A. Floren, R. L. Kitching, E. Medianero, S. E. Miller, E. Gama de Oliveira, J. Orivel, M. Pollet, M. Rapp, S. P. Ribeiro, Y. Roisin, J. B. Schmidt, L. Sorensen, and M. Leponce. 2012. Arthropod diversity in a tropical forest. Science 338:1481–1484.

Bässler, C., H. Halbwachs, P. Karasch, H. Holzer, A. Gminder, L. Krieglsteiner, R. S. Gonzalez, J. Müller, and R. Brandl. 2016. Mean reproductive traits of fungal assemblages are correlated with resource availability. Ecology and Evolution 6:582–592.

Basu, P. 1997. Seasonal and spatial patterns in ground foraging ants in a rain rorest in the Western Ghats, India. Biotropica 29:489–500.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software

67:1–48.
Beck, C. B. 1966. On the origin of gymnosperms. Taxon 15:337–339.
Beck, J., C. M. McCain, J. C. Axmacher, L. A. Ashton, F. Bärtschi, G. Brehm, S.-W. Choi, O. Cizek, R. K. Colwell, K. Fiedler, C. L. Francois, S. Highland, J. D. Holloway, J. Intachat, T. Kadlec, R. L. Kitching, S. C. Maunsell, T. Merckx, A. Nakamura, E. Odell, W. Sang, P. S. Toko, J. Zamecnik, Y. Zou, and V. Novotny. 2017. Elevational species richness gradients in a hyperdiverse insect taxon: a global meta-study on geometrid moths. Global Ecology and Biogeography 26:412–424.
Bell, C. D., D. E. Soltis, and P. S. Soltis. 2010. The age and diversification of the angiosperms re-revisited. American Journal of Botany 97:1296–1303.
de Bello, F., S. Lavorel, S. Díaz, R. Harrington, J. H. C. Cornelissen, R. D. Bardgett, M. P. Berg, P. Cipriotti, C. K. Feld, D. Hering, P. Martins da Silva, S. G. Potts, L. Sandin, J. P. Sousa, J. Storkey, D. A. Wardle, and P. A. Harrison. 2010. Towards an assessment of multiple ecosystem processes and services via functional traits. Biodiversity and Conservation 19:2873–2893.
Belovsky, G. E. 1997. Optimal foraging and community structure: the allometry of herbivore food selection and competition. Evolutionary Ecology 11:641–672.
Belovsky, G. E., and J. B. Slade. 1993. The role of vertebrate and invertebrate predators in a grasshopper community. Oikos 68:193–201.
Bendix, J., H. Behling, T. Peters, M. Richter, and E. Beck. 2010. Functional biodiversity and climate change along an altitudinal gradient in a tropical mountain rainforest. Pages 239–268*in* T. Tscharntke, C. Leuschner, E. Veldkamp, H. Faust, E. Guhardja, and A. Bidin, editors.Tropical rainforests and agroforests under global change. Springer, Berlin, Heidelberg.
Bendix, J., R. Rollenbeck, P. Fabian, P. Emck, M. Richter, and E. Beck. 2008a. Climate Variability. Pages 281–290*in* E. Beck, J. Bendix, I. Kottke, F. Makeschin, and R. Mosandl, editors.Ecological studies, vol 198: Gradients in a tropical mountain ecosystem of Ecuador. Springer, Berlin Heidelberg.
Bendix, J., R. Rollenbeck, D. Göttlicher, and J. Cermak. 2006. Cloud occurrence and cloud properties in Ecuador. Climate Research 30:133–147.
Bendix, J., R. Rollenbeck, M. Richter, P. Fabian, and P. Emck. 2008b. Climate. Pages 63–73*in* E. Beck, J. Bendix, I. Kottke, F. Makeschin, and R. Mosandl, editors.Ecological studies, vol 198: Gradients in a tropical mountain ecosystem of Ecuador. Springer, Berlin Heidelberg.
Bennet-Clark, H. C. 1990. Jumping in Orthoptera. Pages 173–203*in* R. F. Chapman and A. Joern, editors.Biology of grasshoppers. John Wiley & Sons.
Bergmann, C. 1847. Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. Göttinger Stud. 1:595–708.
Berner, D., C. Körner, and W. U. Blanckenhorn. 2004. Grasshopper populations across 2000 m of altitude: is there life history adaptation? Ecography 27:733–740.
Bidau, C. J. 2014. Patterns in Orthoptera biodiversity. I. Adaptations in ecological and evolutionary contexts. Journal of Insect Biodiversity 2:1–39.
Biggs, R., M. Schlüter, D. Biggs, E. L. Bohensky, S. BurnSilver, G. Cundill, V. Dakos, T. M. Daw, L. S. Evans, K. Kotschy, A. M. Leitch, C. Meek, A. Quinlan, C. Raudsepp-Hearne, M. D. Robards, M. L. Schoon, L. Schultz, and P. C. West. 2012. Toward principles for enhancing the resilience of ecosystem services. Annual Review of Environment and Resources 37:421–448.
Bihn, J. H., G. Gebauer, and R. Brandl. 2010. Loss of functional diversity of ant assemblages in secondary tropical forests. Ecology 91:782–792.
Bihn, J. H., M. Verhaagh, M. Brändle, and R. Brandl. 2008. Do secondary forests act as refuges for old growth forest animals? Recovery of ant diversity in the Atlantic forest of Brazil. Biological Conservation 141:733–743.
Bishop, T. R., M. P. Robertson, H. Gibb, B. J. van Rensburg, B. Braschler, S. L. Chown, S. H. Foord, T. C. Munyai, I. Okey, P. G. Tshivhandekano, V. Werenkraut, and C. L. Parr. 2016. Ant assemblages have darker and larger members in cold environments. Global Ecology and Biogeography 25:1489–1499.
Bishop, T. R., M. P. Robertson, B. J. van Rensburg, and C. L. Parr. 2014. Elevation-diversity patterns through space and time: ant communities of the Maloti-Drakensberg Mountains of southern Africa. Journal of Biogeography 41:2256–2268.
Blackburn, T. M., and K. J. Gaston. 2001, July 7. Linking patterns in macroecology. Blackwell Science Ltd.
Blanckenhorn, W. U., and M. Demont. 2004.

Bergmann and converse Bergmann latitudinal clines in arthropods: two ends of a continuum? Integrative and Comparative Biology 44:413–424.

Blois, J. L., J. W. Williams, M. C. Fitzpatrick, S. T. Jackson, and S. Ferrier. 2013. Space can substitute for time in predicting climate-change effects on biodiversity. Proceedings of the National Academy of Sciences of the United States of America 110:9374–9.

Blonder, B., C. Lamanna, C. Violle, and B. J. Enquist. 2014. The n -dimensional hypervolume. Global Ecology and Biogeography 23:595–609.

De Bodt, S., S. Maere, and Y. Van de Peer. 2005. Genome duplication and the origin of angiosperms. Trends in Ecology & Evolution 20:591–7.

Botes, A., M. A. McGeoch, H. G. Robertson, A. Niekerk, H. P. Davids, and S. L. Chown. 2006. Ants, altitude and change in the northern cape floristic region. Journal of Biogeography 33:71–90.

Boucher-Lalonde, V., R. X. De Camargo, J.-M. Fortin, S. Khair, R. I. So, H. Vázquez Rivera, D. Watson, J. Zuloaga, and D. J. Currie. 2015. The weakness of evidence supporting tropical niche conservatism as a main driver of current richness-temperature gradients. Global Ecology and Biogeography 24:795–803.

Branson, D. H. 2005. Direct and indirect effects of avian predation on grasshopper communities in northern mixed-grass prairie. Environmental Entomology 34:1114–1121.

Brehm, G. 2002. Diversity of geometrid moths in a montane rainforest in Ecuador. Universität Bayreuth.

Briggs, J. C. 1995. Global Biogeography. Developmen. Elsevier Science B.V., Amsterdam.

Brook, B., N. Sodhi, and C. Bradshaw. 2008. Synergies among extinction drivers under global change. Trends in Ecology & Evolution 23:453–460.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. Ecology 85:1771–1789.

Bruhl, C. A., T. Eltz, K. E. Linsenmair, C. A. Brühl, T. Eltz, and K. E. Linsenmair. 2003. Size does matter - effects of tropical rainforest fragmentation on the leaf litter ant community in Sabah, Malaysia. Biodiversity & Conservation 12:1371–1389.

Bryant, J. A., C. Lamanna, H. Morlon, A. J. Kerkhoff, B. J. Enquist, and J. L. Green. 2008. Microbes on mountainsides: contrasting elevational patterns of bacterial and plant diversity. Proceedings of the National Academy of Sciences of the United States of America 105:11505–11511.

Bucher, R., H. Binz, F. Menzel, and M. H. Entling. 2014. Effects of spider chemotactile cues on arthropod behavior. Journal of Insect Behavior 27:567–580.

Buckley, L. B., and W. Jetz. 2008. Linking global turnover of species and environments. Proceedings of the National Academy of Sciences of the United States of America 105:17836–41.

Burrows, M., and G. P. Sutton. 2008. The effect of leg length on jumping performance of short- and long-legged leafhopper insects. Journal of Experimental Biology 211.

Cadotte, M., C. H. Albert, and S. C. Walker. 2013. The ecology of differences: assessing community assembly with trait and evolutionary distances. Ecology Letters 16:1234–1244.

Cadotte, M. W. 2013. Experimental evidence that evolutionarily diverse assemblages result in higher productivity. Proceedings of the National Academy of Sciences of the United States of America 110:8996–9000.

Cadotte, M. W., B. J. Cardinale, and T. H. Oakley. 2008. Evolutionary history and the effect of biodiversity on plant productivity. Proceedings of the National Academy of Sciences of the United States of America 105:17012–7.

Cadotte, M. W., K. Carscadden, and N. Mirotchnick. 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. Journal of Applied Ecology 48:1079–1087.

Cadotte, M. W., J. Cavender-Bares, D. Tilman, and T. H. Oakley. 2009a. Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. PLoS ONE 4:e5695.

Cadotte, M. W., M. a. Hamilton, and B. R. Murray. 2009b. Phylogenetic relatedness and plant invader success across two spatial scales. Diversity and Distributions 15:481–488.

Cadotte, M. W., and C. M. Tucker. 2017. Should environmental filtering be abandoned? Trends in Ecology & Evolution 32:429–437.

Cahill, J. F., S. W. Kembel, E. G. Lamb, and P. A. Keddy. 2008. Does phylogenetic relatedness influence the strength of competition among vascular plants? Perspectives in Plant Ecology, Evolution

and Systematics 10:41–50.
Cardinale, B. J., J. E. Duffy, A. Gonzalez, D. U. Hooper, C. Perrings, P. Venail, A. Narwani, G. M. Mace, D. Tilman, D. A. Wardle, A. P. Kinzig, G. C. Daily, M. Loreau, J. B. Grace, A. Larigauderie, D. S. Srivastava, and S. Naeem. 2012. Biodiversity loss and its impact on humanity. Nature 486:59–67.
Cardinale, B. J., K. L. Matulich, D. U. Hooper, J. E. Byrnes, E. Duffy, L. Gamfeldt, P. Balvanera, M. I. O'Connor, and A. Gonzalez. 2011. The functional role of producer diversity in ecosystems. American Journal of Botany 98:572–592.
Carignan, V., and M.-A. Villard. 2002. Selecting indicator species to monitor ecological integrity: a review. Environmental Monitoring and Assessment 78:45–61.
Carpenter, B., A. Gelman, M. D. Hoffman, D. Lee, B. Goodrich, M. Betancourt, M. Brubaker, J. Guo, P. Li, and A. Riddell. 2017. Stan : a probabilistic programming language. Journal of Statistical Software 76.
Carvalho, K. S., and H. L. Vasconcelos. 1999. Forest fragmentation in central Amazonia and its effects on litter-dwelling ants. Biological Conservation 91:151–157.
Castro, F. S. de, A. B. Gontijo, P. D. T. A. Castro, and S. P. Ribeiro. 2012. Annual and seasonal changes in the structure of litter-dwelling ant assemblages (Hymenoptera: Formicidae) in Atlantic semideciduous forests. Psyche 2012:1–12.
Cavender-Bares, J., K. H. Kozak, P. V. A. Fine, and S. W. Kembel. 2009. The merging of community ecology and phylogenetic biology. Ecology Letters 12:693–715.
Ceballos, G., P. R. Ehrlich, A. D. Barnosky, A. García, R. M. Pringle, and T. M. Palmer. 2015. Accelerated modern human–induced species losses: entering the sixth mass extinction. Science Advances 1.
Chapin III, F. S., B. H. Walker, R. J. Hobbs, D. U. Hooper, J. H. Lawton, O. E. Sala, and D. Tilman. 1997. Biotic control over the functioning of ecosystems. Science 277:500–504.
Chapin III, F. S., E. S. Zavaleta, V. T. Eviner, R. L. Naylor, P. M. Vitousek, H. L. Reynolds, D. U. Hooper, S. Lavorel, O. E. Sala, S. E. Hobbie, M. C. Mack, and S. Díaz. 2000. Consequences of changing biodiversity. Nature 405:234–242.
Chazdon, R. L., S. Careaga, C. Webb, and O. Vargas. 2003. Community and phylogenetic structure of reproductive traits of woody species in wet tropical forests. Ecological Monographs 73:331–348.
Chazdon, R. L., C. A. Harvey, O. Komar, D. M. Griffith, B. G. Ferguson, M. Martínez-Ramos, H. Morales, R. Nigh, L. Soto-Pinto, M. Van Breugel, and S. M. Philpott. 2009. Beyond reserves: a research agenda for conserving biodiversity in human-modified tropical landscapes. Biotropica 41:142–153.
Chen, I.-C., J. K. Hill, R. Ohlemüller, D. B. Roy, and C. D. Thomas. 2011. Rapid range shifts of species associated with high levels of climate warming. Science 333:1024–1026.
Chen, I.-C., H.-J. Shiu, S. Benedick, J. D. Holloway, V. K. Chey, H. S. Barlow, J. K. Hill, and C. D. Thomas. 2009. Elevation increases in moth assemblages over 42 years on a tropical mountain. Proceedings of the National Academy of Sciences of the United States of America 106:1479–83.
Chown, S. L., and K. J. Gaston. 1999. Exploring links between physiology and ecology at macro-scales: the role of respiratory metabolism in insects. Biological Reviews 74:87–120.
Chown, S. L., and K. J. Gaston. 2010. Body size variation in insects: a macroecological perspective. Biological reviews of the Cambridge Philosophical Society 85:139–69.
Clapham, M. E., and J. A. Karr. 2012. Environmental and biotic controls on the evolutionary history of insect body size. Proceedings of the National Academy of Sciences of the United States of America 109:10927–30.
Clarke, D. A., P. H. York, M. A. Rasheed, and T. D. Northfield. 2017. Does biodiversity–ecosystem function literature neglect tropical ecosystems? Trends in Ecology & Evolution 32:320–323.
Colwell, R. K., G. Brehm, C. L. Cardelus, A. C. Gilman, and J. T. Longino. 2008. Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. Science 322:258–261.
Colwell, R. K., A. Chao, N. J. Gotelli, S.-Y. Lin, C. X. Mao, R. L. Chazdon, and J. T. Longino. 2012. Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. Journal of Plant Ecology 5:3–21.
Colwell, R. K., N. J. Gotelli, L. A. Ashton, J. Beck, G. Brehm, T. M. Fayle, K. Fiedler, M. L. Forister, M. Kessler, R. L. Kitching, P. Klimes, J. Kluge, J. T. Longino, S. C. Maunsell, C. M. McCain, J. Moses, S.

Noben, K. Sam, L. Sam, A. M. Shapiro, X. Wang, and V. Novotny. 2016. Midpoint attractors and species richness: modelling the interaction between environmental drivers and geometric constraints. Ecology Letters 19:1009–1022.

Cooper, W. 2006. Risk factors and escape strategy in the grasshopper *Dissosteira carolina*. Behaviour 143:1201–1218.

Culmsee, H., and C. Leuschner. 2013. Consistent patterns of elevational change in tree taxonomic and phylogenetic diversity across Malesian mountain forests. Journal of Biogeography 40:1997–2010.

Curatola Fernández, G., W. Obermeier, A. Gerique, M. Sandoval, L. Lehnert, B. Thies, and J. Bendix. 2015. Land cover change in the Andes of southern Ecuador—patterns and drivers. Remote Sensing 7:2509–2542.

Dale, V. H., and S. C. Beyeler. 2001. Challenges in the development and use of ecological indicators. Ecological Indicators 1:3–10.

Dangles, O., C. Magal, D. Pierre, A. Olivier, and J. Casas. 2005. Variation in morphology and performance of predator-sensing system in wild cricket populations. Journal of Experimental Biology 208.

Darwin, C. 1859. On the origin of species by means of natural selection. John Murray, London.

Davidson, D. W. 1977. Foraging ecology and community organization in desert seed-eating ants. Ecology 58:725–737.

Davidson, D. W. 1998. Resource discovery versus resource domination in ants: a functional mechanism for breaking the trade-off. Ecological Entomology 23:484–490.

Davies, T. J., T. G. Barraclough, M. W. Chase, P. S. Soltis, D. E. Soltis, and V. Savolainen. 2004. Darwin's abominable mystery: insights from a supertree of the angiosperms. Proceedings of the National Academy of Sciences 101:1904–1909.

Davies, T. J., N. J. B. Kraft, N. Salamin, and E. M. Wolkovich. 2012. Incompletely resolved phylogenetic trees inflate estimates of phylogenetic conservatism. Ecology 93:242–247.

Dehling, D. M., P. Jordano, H. M. Schaefer, K. Böhning-Gaese, and M. Schleuning. 2016. Morphology predicts species' functional roles and their degree of specialization in plant–frugivore interactions. Proceedings of the Royal Society of London B: Biological Sciences 283.

Delsinne, T., T. Arias-Penna, and M. Leponce. 2013. Effect of rainfall exclusion on ant assemblages in montane rainforests of Ecuador. Basic and Applied Ecology 14:357–365.

Denno, R. F., C. Gratton, H. Döbel, and D. L. Finke. 2003. Predation risk affects relative strength of top-down and bottom-up impacts on insect herbivores. Ecology 84:1032–1044.

Denno, R. F., G. K. Roderick, K. L. Olmstead, and H. G. Döbel. 1991. Density-related migration in planthoppers (Homoptera: Delphacidae): the role of habitat persistence. The American Naturalist 138:1513–1541.

Devictor, V., D. Mouillot, C. Meynard, F. Jiguet, W. Thuiller, and N. Mouquet. 2010. Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. Ecology Letters 13:no-no.

Díaz, S., and M. Cabido. 2001. Vive la différence: plant functional diversity matters to ecosystem processes. Trends in Ecology & Evolution 16:646–655.

Díaz, S., S. Lavorel, F. de Bello, F. Quétier, K. Grigulis, and T. M. Robson. 2007. Incorporating plant functional diversity effects in ecosystem service assessments. Proceedings of the National Academy of Sciences of the United States of America 104:20684–9.

Dillon, M. E., M. R. Frazier, and R. Dudley. 2006. Into thin air: physiology and evolution of alpine insects. Integrative and comparative biology 46:49–61.

Domínguez, D. F., M. Bustamante, R. Albuja, A. Castro, J. E. Lattke, and D. A. Donoso. 2016. COI barcodes for ants (Hymenoptera: Formicidae) of drylands in the south of Ecuador. Ecosistemas 25:76–78.

Donoso, D. A. 2017. Tropical ant communities are in long-term equilibrium. Ecological Indicators 83:515–523.

Donoso, D. A., and G. Ramón. 2009. Composition of a high diversity leaf litter ant community (Hymenoptera: Formicidae) from an Ecuadorian pre-montane rainforest. Annales de la Société entomologique de France (N.S.) 45:487–499.

Dossa, G. G. O., E. Paudel, J. Fujinuma, H. Yu, W. Chutipong, Y. Zhang, S. Paz, and R. D. Harrison. 2013. Factors determining forest diversity and biomass on a tropical volcano, Mt. Rinjani, Lombok, Indonesia. PLoS ONE 8:e67720.

Dudley, R. 2002. Mechanisms and implications of animal flight maneuverability.

Integrative and Comparative Biology 42:135–140.
Edwards, D. P., J. A. Tobias, D. Sheil, E. Meijaard, and W. F. Laurance. 2014. Maintaining ecosystem function and services in logged tropical forests. Trends in Ecology & Evolution 29:511–520.
Emerson, B. C., and R. G. Gillespie. 2008. Phylogenetic analysis of community assembly and structure over space and time. Trends in Ecology & Evolution 23:619–630.
Eterovick, P. C., J. E. C. Figueira, and J. Vasconcellos-Neto. 1997. Cryptic coloration and choice of escape microhabitats by grasshoppers (Orthoptera: Acrididae). Biological Journal of the Linnean Society 61:485–499.
Fartmann, T., B. Krämer, F. Stelzner, and D. Poniatowski. 2012. Orthoptera as ecological indicators for succession in steppe grassland. Ecological Indicators 20:337–344.
Fayle, T. M., E. C. Turner, Y. Basset, R. M. Ewers, G. Reynolds, and V. Novotny. 2015. Whole-ecosystem experimental manipulations of tropical forests. Trends in Ecology & Evolution 30:334–346.
Field, R., B. A. Hawkins, H. V. Cornell, D. J. Currie, J. A. F. Diniz-Filho, J.-F. Guégan, D. M. Kaufman, J. T. Kerr, G. G. Mittelbach, T. Oberdorff, E. M. O'Brien, and J. R. G. Turner. 2009. Spatial species-richness gradients across scales: a meta-analysis. Journal of Biogeography 36:132–147.
Fielding, D. J. 2004. Intraspecific competition and spatial heterogeneity alter life history traits in an individual-based model of grasshoppers. Ecological Modelling 175:169–187.
Floren, A., A. Biun, and E. Linsenmair. 2002. Arboreal ants as key predators in tropical lowland rainforest trees. Oecologia 131:137–144.
Flynn, D. F. B., N. Mirotchnick, M. Jain, M. I. Palmer, and S. Naeem. 2011. Functional and phylogenetic diversity as predictors of biodiversity--ecosystem-function relationships. Ecology 92:1573–1581.
Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin, M. T. Coe, G. C. Daily, H. K. Gibbs, J. H. Helkowski, T. Holloway, E. A. Howard, C. J. Kucharik, C. Monfreda, J. A. Patz, I. C. Prentice, N. Ramankutty, and P. K. Snyder. 2005. Global consequences of land use. Science 309:570–574.
Folgarait, P. J. 1998. Ant biodiversity and its relationship to ecosystem functioning: a review. Biodiversity & Conservation 7:1221–1244.
Forest, F., R. Grenyer, M. Rouget, T. J. Davies, R. M. Cowling, D. P. Faith, A. Balmford, J. C. Manning, Ş. Procheş, M. van der Bank, G. Reeves, T. A. J. Hedderson, and V. Savolainen. 2007. Preserving the evolutionary potential of floras in biodiversity hotspots. Nature 445:757–760.
Fotso Kuate, A., R. Hanna, M. Tindo, S. Nanga, and P. Nagel. 2015. Ant diversity in dominant vegetation types of Southern Cameroon. Biotropica 47:94–100.
Fowler, H. G., L. C. Forti, C. R. F. Brandao, J. H. C. Delabie, H. L. Vasconcelos, A. R. Panizzi, and J. R. P. Parra. 1991. Ecologia nutricional de formigas. Pages 131–223*in* A. R. Oanizzi and J. R. P. Parra, editors.Ecologia nutricional de insetos. Manole São Paulo.
Frainer, A., B. G. McKie, and B. Malmqvist. 2014. When does diversity matter? Species functional diversity and ecosystem functioning across habitats and seasons in a field experiment. Journal of Animal Ecology 83:460–469.
Funk, J. L., J. E. Larson, G. M. Ames, B. J. Butterfield, J. Cavender-Bares, J. Firn, D. C. Laughlin, A. E. Sutton-Grier, L. Williams, and J. Wright. 2017. Revisiting the Holy Grail: using plant functional traits to understand ecological processes. Biological Reviews 92:1156–1173.
Gagic, V., I. Bartomeus, T. Jonsson, A. Taylor, C. Winqvist, C. Fischer, E. M. Slade, I. Steffan-Dewenter, M. Emmerson, S. G. Potts, T. Tscharntke, W. Weisser, and R. Bommarco. 2015. Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. Proceedings. Biological sciences 282:20142620.
Galtier, J., and N. P. Rowe. 1989. A primitive seed-like structure and its implications for early gymnosperm evolution. Nature 340:225–227.
Garcia, R. A., M. Cabeza, C. Rahbek, and M. B. Araujo. 2014. Multiple dimensions of climate change and their implications for biodiversity. Science 344:1247579.
Gastauer, M., J. A. A. Meira-Neto, M. Gastauer, and J. A. A. Meira-Neto. 2016. An enhanced calibration of a recently released megatree for the analysis of phylogenetic diversity. Brazilian Journal of Biology 76:619–628.
Gaston, K. J. 2000. Global patterns in biodiversity. Nature 405:220–227.
Gaston, K. J. 2007. Latitudinal gradient in

species richness. Current Biology 17:R574.
Gaston, K. J., and T. M. Blackburn. 1996. The tropics as a museum of biological diversity: an analysis of the New World avifauna. Proceedings of the Royal Society of London B: Biological Sciences 263:63–68.
Genung, M. A., J. Fox, N. M. Williams, C. Kremen, J. Ascher, J. Gibbs, and R. Winfree. 2017. The relative importance of pollinator abundance and species richness for the temporal variance of pollination services. Ecology 98:1807–1816.
Gerhold, P., J. F. Cahill, M. Winter, I. V. Bartish, and A. Prinzing. 2015. Phylogenetic patterns are not proxies of community assembly mechanisms (they are far better). Functional Ecology 29:600–614.
Gibb, H., and C. L. Parr. 2013. Does structural complexity determine the morphology of assemblages? An experimental test on three continents. PLOS ONE 8:e64005.
Gibb, H., N. J. Sanders, R. R. Dunn, S. Watson, M. Photakis, S. Abril, A. N. Andersen, E. Angulo, I. Armbrecht, X. Arnan, F. B. Baccaro, T. R. Bishop, R. Boulay, C. Castracani, I. Del Toro, T. Delsinne, M. Diaz, D. A. Donoso, M. L. Enriquez, T. M. Fayle, D. H. Feener, M. C. Fitzpatrick, C. Gomez, D. A. Grasso, S. Groc, B. Heterick, B. D. Hoffmann, L. Lach, J. Lattke, M. Leponce, J.-P. Lessard, J. Longino, A. Lucky, J. Majer, S. B. Menke, D. Mezger, A. Mori, T. C. Munyai, O. Paknia, J. Pearce-Duvet, M. Pfeiffer, S. M. Philpott, J. L. P. de Souza, M. Tista, H. L. Vasconcelos, M. Vonshak, and C. L. Parr. 2015a. Climate mediates the effects of disturbance on ant assemblage structure. Proceedings of the Royal Society B 282:20150418.
Gibb, H., J. Stoklosa, D. I. Warton, A. M. Brown, N. R. Andrew, and S. A. Cunningham. 2015b. Does morphology predict trophic position and habitat use of ant species and assemblages? Oecologia 177:519–531.
Giehl, E. L. H., and J. A. Jarenkow. 2012. Niche conservatism and the differences in species richness at the transition of tropical and subtropical climates in South America. Ecography 35:933–943.
Gollan, J. R., L. L. De Bruyn, N. Reid, D. Smith, and L. Wilkie. 2011. Can ants be used as ecological indicators of restoration progress in dynamic environments? A case study in a revegetated riparian zone. Ecological Indicators 11:1517–1525.
Gossner, M. M., C. R. Fonseca, E. Pašalić, M. Türke, M. Lange, and W. W. Weisser. 2014. Limitations to the use of arthropods as temperate forests indicators. Biodiversity and Conservation 23:945–962.
Grace, J. B., T. M. Anderson, E. W. Seabloom, E. T. Borer, P. B. Adler, W. S. Harpole, Y. Hautier, H. Hillebrand, E. M. Lind, M. Pärtel, J. D. Bakker, Y. M. Buckley, M. J. Crawley, E. I. Damschen, K. F. Davies, P. A. Fay, J. Firn, D. S. Gruner, A. Hector, J. M. H. Knops, A. S. MacDougall, B. A. Melbourne, J. W. Morgan, J. L. Orrock, S. M. Prober, and M. D. Smith. 2016. Integrative modelling reveals mechanisms linking productivity and plant species richness. Nature 529:390–393.
Graham, A. 2011. The age and diversification of terrestrial New World ecosystems through Cretaceous and Cenozoic time. American Journal of Botany 98:336–351.
Graham, C. H., A. C. Carnaval, C. D. Cadena, K. R. Zamudio, T. E. Roberts, J. L. Parra, C. M. Mccain, R. C. K. Bowie, C. Moritz, S. B. Baines, C. J. Schneider, J. Vanderwal, C. Rahbek, K. H. Kozak, and N. J. Sanders. 2014. The origin and maintenance of montane diversity: integrating evolutionary and ecological processes. Ecography 37:711–719.
Graham, C. H., and P. V. A. Fine. 2008. Phylogenetic beta diversity: linking ecological and evolutionary processes across space in time. Ecology Letters 11:1265–1277.
Graham, C. H., J. L. Parra, B. A. Tinoco, F. G. Stiles, and J. A. McGuire. 2012. Untangling the influence of ecological and evolutionary factors on trait variation across hummingbird assemblages. Ecology 93:S99–S111.
Green, A. J. 2001. Mass/length residuals: measures of body condition or generators of spurious results? Ecology 82:1473–1483.
Griffin, J. N., V. Méndez, A. F. Johnson, S. R. Jenkins, and A. Foggo. 2009. Functional diversity predicts overyielding effect of species combination on primary productivity. Oikos 118:37–44.
Grossman, J. J., J. Cavender-Bares, S. E. Hobbie, P. B. Reich, and R. A. Montgomery. 2017. Species richness and traits predict overyielding in stem growth in an early-successional tree diversity experiment. Ecology 38:42–49.
Haddad, N. M., L. A. Brudvig, J. Clobert, K. F. Davies, A. Gonzalez, R. D. Holt, T. E. Lovejoy, J. O. Sexton, M. P. Austin, C. D. Collins, W. M. Cook, E. I. Damschen, R. M. Ewers, B. L. Foster, C. N. Jenkins, A. J. King, W. F. Laurance, D. J. Levey, C. R. Margules, B. A. Melbourne, A. O. Nicholls,

J. L. Orrock, D.-X. Song, and J. R. Townshend. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Science Advances 1.
Halbritter, A. H., J. M. Alexander, P. J. Edwards, and R. Billeter. 2013. How comparable are species distributions along elevational and latitudinal climate gradients? Global Ecology and Biogeography 22:1228–1237.
Hannah, L., G. F. Midgley, T. Lovejoy, W. J. Bond, M. Bush, J. C. Lovett, D. Scott, and F. I. Woodward. 2002. Conservation of Biodiversity in a changing climate. Conservation Biology 16:264–268.
Hardy, O. J., P. Couteron, F. Munoz, B. R. Ramesh, and R. Pélissier. 2012. Phylogenetic turnover in tropical tree communities: impact of environmental filtering, biogeography and mesoclimatic niche conservatism. Global Ecology and Biogeography 21:1007–1016.
Harrison, S., and E. Bruna. 1999. Habitat fragmentation and large-scale conservation: what do we know for sure? Ecography 22:225–232.
Harrison, X. A. 2014. Using observation-level random effects to model overdispersion in count data in ecology and evolution. PeerJ 2:e616.
van der Have, T. M., and G. de Jong. 1996. Adult size in ectotherms: temperature effects on growth and differentiation. Journal of Theoretical Biology 183:329–340.
Hawkins, B. A., B. Leroy, M. Á. Rodríguez, A. Singer, B. Vilela, F. Villalobos, X. Wang, and D. Zelený. 2017. Structural bias in aggregated species-level variables driven by repeated species co-occurrences: a pervasive problem in community and assemblage data. Journal of Biogeography 44:1199–1211.
Hawkins, B. A., E. E. Porter, and J. A. Felizola Diniz-Filho. 2003. Productivity and history as predictors of the latitudinal diversity gradient of terrestrial birds. Ecology 84:1608–1623.
Hawkins, B. A., M. Á. Rodríguez, and S. G. Weller. 2011. Global angiosperm family richness revisited: linking ecology and evolution to climate. Journal of Biogeography 38:1253–1266.
Hawkins, B. A., M. Rueda, T. F. Rangel, R. Field, and J. A. F. Diniz-Filho. 2014. Community phylogenetics at the biogeographical scale: cold tolerance, niche conservatism and the structure of North American forests. Journal of Biogeography 41:23–38.
Hector, A., and R. Bagchi. 2007. Biodiversity and ecosystem multifunctionality. Nature 448:188–190.
Hemp, A. 2006. Continuum or zonation? Altitudinal gradients in the forest vegetation of Mt. Kilimanjaro. Plant Ecology 184:27–42.
Hemp, C., and A. Hemp. 2003. *Saltatoria coenoses* of high-altitude grasslands on Mt. Kilimanjaro, Tanzania (Orthoptera: Saltatoria). Ecotropica 9:71–97.
Hill, M. O., and H. G. Gauch. 1980. Detrended correspondence analysis: an improved ordination technique. Vegetatio 42:47–58.
Hillebrand, H. 2004. On the generality of the latitudinal diversity gradient. The American Naturalist 163:192–211.
Hodkinson, I. D. 2005. Terrestrial insects along elevation gradients: species and community responses to altitude. Biological Reviews 80:489–513.
Hoffmann, B. D. 2010. Using ants for rangeland monitoring: Global patterns in the responses of ant communities to grazing. Ecological Indicators 10:105–111.
Hoffmann, B. D., and A. N. Andersen. 2003. Responses of ants to disturbance in Australia, with particular reference to functional groups. Austral Ecology 28:444–464.
Hölldobler, B., and E. O. Wilson. 1990. The Ants. Harvard University Press.
Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. Theoretical Population Biology 12:197–229.
Homeier, J., S. Breckle, S. Günter, R. Rollenbeck, and C. Leuschner. 2010. Tree diversity, forest structure and productivity along altitudinal and topographical gradients in a species rich Ecuadorian montane rain forest. Biotropica 42:140–148.
Homeier, J., F. A. Werner, S. R. Gradstein, S. W. Breckle, and M. Richter. 2008. Flora and fungi: composition and function. Pages 87–100 *in* E. Beck, J. Bendix, I. Kottke, F. Makeschin, and R. Mosandl, editors.Gradients in a Tropical Mountain Ecosystem of Ecuador. Springer, Berlin, Heidelberg.
Hooper, D. U., E. C. Adair, B. J. Cardinale, J. E. K. Byrnes, B. A. Hungate, K. L. Matulich, A. Gonzalez, J. E. Duffy, L. Gamfeldt, and M. I. O'Connor. 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature 486:105.
Hooper, D. U., F. S. Chapin, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setälä, A. J. Symstad, J. Vandermeer, and D. A. Wardle. 2005. Effects of biodiversity

on ecosystem functioning: a consensus of current knowledge. Ecological Monographs 75:3–35.
Hoorn, C., F. P. Wesselingh, H. ter Steege, M. A. Bermudez, A. Mora, J. Sevink, I. Sanmartín, A. Sanchez-Meseguer, C. L. Anderson, J. P. Figueiredo, C. Jaramillo, D. Riff, F. R. Negri, H. Hooghiemstra, J. Lundberg, T. Stadler, T. Särkinen, and A. Antonelli. 2010. Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. Science 330:927–931.
Hothorn, T., F. Bretz, and P. Westfall. 2008. Simultaneous inference in general parametric models. Biometrical Journal 50:346–363.
Houghton, J., G. Jenkins, and J. Ephraums. 1990. Climate change: the IPCC scientific assessment. Cambridge University Press.
Howe, A., G. L. Lövei, and G. Nachman. 2009. Dummy caterpillars as a simple method to assess predation rates on invertebrates in a tropical agroecosystem. Entomologia Experimentalis et Applicata 131:325–329.
Huang, S., K. Roy, and D. Jablonski. 2014. Do past climate states influence diversity dynamics and the present-day latitudinal diversity gradient? Global Ecology and Biogeography 23:530–540.
Hughes, L. 2000. Biological consequences of global warming: is the signal already apparent? Trends in Ecology & Evolution 15:56–61.
Hunter, M. D. 2002. Landscape structure, habitat fragmentation, and the ecology of insects. Agricultural and Forest Entomology 4:159–166.
Hurlbert, A. H., F. Ballantyne, and S. Powell. 2008. Shaking a leg and hot to trot: the effects of body size and temperature on running speed in ants. Ecological Entomology 33:144–154.
Hurlbert, S. H. 1971. The nonconcept of species diversity: a critique and alternative parameters. Ecology 52:577–586.
Huston, M. A., and S. Wolverton. 2011. Regulation of animal size by eNPP, Bergmann's rule, and related phenomena. Ecological Monographs 81:349–405.
Intergovernmental Panel on Climate Change. 2007. Climate change 2007 - the physical science basis - contribution of working group I to the fourth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press.
Isbell, F., P. B. Reich, D. Tilman, S. E. Hobbie, S. Polasky, and S. Binder. 2013. Nutrient enrichment, biodiversity loss, and consequent declines in ecosystem productivity. Proceedings of the National Academy of Sciences of the United States of America 110:11911–6.
Janes, S. W. 1994. Variation in the species composition and mean body size of an avian foliage-gleaning guild along an elevational gradient: correlation with arthropod body size. Oecologia 98:369–378.
Jansson, R., G. Rodríguez-Castañeda, and L. E. Harding. 2013. What can multiple phylogenies say about the latitudinal diversity gradient? A new look at the tropical conservatism, out of the tropics, and diversification rate hypotheses. Evolution 67:1741–1755.
Jantz, N., J. Homeier, and H. Behling. 2014. Representativeness of tree diversity in the modern pollen rain of Andean montane forests. Journal of Vegetation Science 25:481–490.
Jayatilaka, P., A. Narendra, S. F. Reid, P. Cooper, and J. Zeil. 2011. Different effects of temperature on foraging activity schedules in sympatric Myrmecia ants. The Journal of experimental biology 214:2730–2738.
Jenkins, C. N., N. J. Sanders, A. N. Andersen, X. Arnan, C. A. Brühl, X. Cerda, A. M. Ellison, B. L. Fisher, M. C. Fitzpatrick, N. J. Gotelli, A. D. Gove, B. Guénard, J. E. Lattke, J.-P. Lessard, T. P. McGlynn, S. B. Menke, C. L. Parr, S. M. Philpott, H. L. Vasconcelos, M. D. Weiser, and R. R. Dunn. 2011. Global diversity in light of climate change: the case of ants. Diversity and Distributions 17:652–662.
Johnson, M. T. J., and J. R. Stinchcombe. 2007. An emerging synthesis between community ecology and evolutionary biology. Trends in Ecology and Evolutioncology & Evolution 22:250–7.
Jorgensen, P. M., and S. León-Yánez, editors. 1999. Catalogue of the vascular plants of Ecuador. Monogr. Sy. Monogr. Syst. Bot. Missouri Bot. Gard. 75: i-viii, 1-1182.
Kaspari, M. 1996. Worker size and seed size selection by harvester ants in a neotropical forest. Oecologia 105:397–404.
Kaspari, M., L. Alonso, and S. O'Donnell. 2000. Three energy variables predict ant abundance at a geographical scale. Proceedings of the Royal Society B: Biological Sciences 267:485–489.
Kaspari, M., and M. D. Weiser. 1999. The size-grain hypothesis and interspecific scaling in ants. Functional Ecology 13:530–538.
Kaspari, M., M. Yuan, and L. Alonso. 2003. Spatial grain and the causes of regional

diversity gradients in ants. The American Naturalist 161:459–477.
Keddy, P. A. 1992. Assembly and response rules: two goals for predictive community ecology. Journal of Vegetation Science 3:157–164.
Kembel, S. W. 2009. Disentangling niche and neutral influences on community assembly: assessing the performance of community phylogenetic structure tests. Ecology Letters 12:949–960.
Kembel, S. W., P. D. Cowan, M. R. Helmus, W. K. Cornwell, H. Morlon, D. D. Ackerly, S. P. Blomberg, and C. O. Webb. 2010. Picante: R tools for integrating phylogenies and ecology. Bioinformatics 26:1463–1464.
Kerkhoff, A. J., P. E. Moriarty, and M. D. Weiser. 2014. The latitudinal species richness gradient in New World woody angiosperms is consistent with the tropical conservatism hypothesis. Proceedings of the National Academy of Sciences of the United States of America 111:8125–30.
Keroumi, A. El, K. Naamani, H. Soummane, and A. Dahbi. 2012. Seasonal dynamics of ant community structure in the Moroccan Argan Forest. Journal of Insect Science 12:1–19.
Kerr, J. T., and M. Ostrovsky. 2003. From space to species: ecological applications for remote sensing. Trends in Ecology & Evolution 18:299–305.
Kessler, M. 2002. The elevational gradient of Andean plant endemism: varying influences of taxon-specific traits and topography at different taxonomic levels. Journal of Biogeography 29:1159–1165.
Klimes, P., P. Fibich, C. Idigel, and M. Rimandai. 2015. Disentangling the diversity of arboreal ant communities in tropical forest trees. PLOS ONE 10:e0117853.
Klimes, P., C. Idigel, M. Rimandai, T. M. Fayle, M. Janda, G. D. Weiblen, and V. Novotny. 2012. Why are there more arboreal ant species in primary than in secondary tropical forests? Journal of Animal Ecology 81:1103–1112.
Körner, C. 2000. Why are there global gradients in species richness? Mountains might hold the answer. Trends in Ecology & Evolution 15:513–514.
Körner, C. 2007. The use of "altitude" in ecological research. Trends in Ecology & Evolution 22:569–574.
Kozak, K. H., and J. J. Wiens. 2010. Niche conservatism drives elevational diversity patterns in Appalachian salamanders. The American Naturalist 176:40–54.
Kraft, N. J. B., P. B. Adler, O. Godoy, E. C. James, S. Fuller, and J. M. Levine. 2015. Community assembly, coexistence and the environmental filtering metaphor. Functional Ecology 29:592–599.
Kress, W. J., D. L. Erickson, F. A. Jones, N. G. Swenson, R. Perez, O. Sanjur, and E. Bermingham. 2009. Plant DNA barcodes and a community phylogeny of a tropical forest dynamics plot in Panama. Proceedings of the National Academy of Sciences of the United States of America 106:18621–18626.
Kress, W. J., D. L. Erickson, N. G. Swenson, J. Thompson, M. Uriarte, and J. K. Zimmerman. 2010. Advances in the use of DNA barcodes to build a community phylogeny for tropical trees in a Puerto Rican forest dynamics plot. PloS one 5:e15409.
LaBarbera, M. 1989. Analyzing body size as a factor in ecology and evolution. Annual Review of Ecology and Systematics 20:97–117.
Laiolo, P., J. C. Illera, and J. R. Obeso. 2013. Local climate determines intra- and interspecific variation in sexual size dimorphism in mountain grasshopper communities. Journal of Evolutionary Biology 26:2171–83.
Laliberté, E., and P. Legendre. 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology 91:299–305.
Laliberté, E., P. Legendre, and Bill Shipley. 2014. FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-12.
Lamanna, C., B. Blonder, C. Violle, N. J. B. Kraft, B. Sandel, I. Imova, J. C. Donoghue, J.-C. Svenning, B. J. McGill, B. Boyle, V. Buzzard, S. Dolins, P. M. Jorgensen, A. Marcuse-Kubitza, N. Morueta-Holme, R. K. Peet, W. H. Piel, J. Regetz, M. Schildhauer, N. Spencer, B. Thiers, S. K. Wiser, and B. J. Enquist. 2014. Functional trait space and the latitudinal diversity gradient. Proceedings of the National Academy of Sciences 111:13745–13750.
Lamsdell, J. C., C. R. Congreve, M. J. Hopkins, A. Z. Krug, and M. E. Patzkowsky. 2017. Phylogenetic paleoecology: tree-thinking and ecology in deep time. Trends in Ecology & Evolution 32:452–463.
Land, M. F. 1997. Visual acuity in insects. Annual Review of Entomology 42:147–177.
Lavergne, S., N. Mouquet, W. Thuiller, and O. Ronce. 2010. Biodiversity and climate

change: integrating evolutionary and ecological responses of species and communities. Annual Review of Ecology, Evolution, and Systematics 41:321–350.
Lavorel, S., and E. Garnier. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisting the Holy Grail. Functional Ecology 16:545–556.
Lavorel, S., J. Storkey, R. D. Bardgett, F. de Bello, M. P. Berg, X. Le Roux, M. Moretti, C. Mulder, R. J. Pakeman, S. Díaz, and R. Harrington. 2013. A novel framework for linking functional diversity of plants with other trophic levels for the quantification of ecosystem services. Journal of Vegetation Science 24:942–948.
Lawton, J. H. 1999. Are there general laws in ecology? Oikos 84:177–192.
Leal, I. R., B. K. C. Filgueiras, J. P. Gomes, L. Iannuzzi, and A. N. Andersen. 2012. Effects of habitat fragmentation on ant richness and functional composition in Brazilian Atlantic forest. Biodiversity and Conservation 21:1687–1701.
Lebrija-Trejos, E., E. A. Pérez-García, J. A. Meave, F. Bongers, and L. Poorter. 2010. Functional traits and environmental filtering drive community assembly in a species-rich tropical system. Ecology 91:386–398.
Lenoir, J., and J.-C. Svenning. 2015. Climate-related range shifts - a global multidimensional synthesis and new research directions. Ecography 38:15–28.
Letten, A. D., and W. K. Cornwell. 2015. Trees, branches and (square) roots: why evolutionary relatedness is not linearly related to functional distance. Methods in Ecology and Evolution 6:439–444.
Levings, S. C. 1983. Seasonal, annual, and among-site variation in the ground ant community of a deciduous tropical forest: some causes of patchy species distributions. Ecological Monographs 53:435–455.
Lomolino, M. V. 2001. Elevation gradients of species-density: historical and prospective views. Global Ecology and Biogeography 10:3–13.
Longino, J. T., M. G. Branstetter, and R. K. Colwell. 2014. How ants drop out: ant abundance on tropical mountains. PLoS ONE 9:e104030.
Losos, J. B. 2008. Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. Ecology Letters 11:995–1003.
Low, P. A., C. McArthur, and D. F. Hochuli. 2016. It is safe to go out on a limb: within-tree leaf age and location do not alter predation risk for insect herbivores. Austral Entomology 55:284–290.
Low, P. A., K. Sam, C. McArthur, M. R. C. Posa, and D. F. Hochuli. 2014. Determining predator identity from attack marks left in model caterpillars: guidelines for best practice. Entomologia Experimentalis et Applicata 152:120–126.
Lu, Y., J.-H. Ran, D.-M. Guo, Z.-Y. Yang, and X.-Q. Wang. 2014. Phylogeny and divergence times of gymnosperms inferred from single-copy nuclear genes. PLoS ONE 9:e107679.
Luebert, F., and M. Weigend. 2014. Phylogenetic insights into Andean plant diversification. Frontiers in Ecology and Evolution 2:1–17.
Lyashevska, O., and K. D. Farnsworth. 2012. How many dimensions of biodiversity do we need? Ecological Indicators 18:485–492.
Machac, A., M. Janda, R. R. Dunn, and N. J. Sanders. 2011. Elevational gradients in phylogenetic structure of ant communities reveal the interplay of biotic and abiotic constraints on diversity. Ecography 34:364–371.
Maeda, E. E., and P. Hurskainen. 2014. Spatiotemporal characterization of land surface temperature in Mount Kilimanjaro using satellite data. Theoretical and Applied Climatology 118:497–509.
Maherali, H., and J. N. Klironomos. 2007. Influence of phylogeny on fungal community assembly and ecosystem functioning. Science 316.
Mazel, F., F. Guilhaumon, N. Mouquet, V. Devictor, D. Gravel, J. Renaud, M. V. Cianciaruso, R. Loyola, J. A. F. Diniz-Filho, D. Mouillot, and W. Thuiller. 2014. Multifaceted diversity-area relationships reveal global hotspots of mammalian species, trait and lineage diversity. Global Ecology and Biogeography 23:836–847.
McCain, C. M. 2007. Could temperature and water availability drive elevational species richness patterns? A global case study for bats. Global Ecology and Biogeography 16:1–13.
McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. Trends in Ecology & Evolution 21:178–185.
Medeiros, J., D. L. O. Azevedo, M. A. D. Santana, T. R. P. Lopes, and A. Araújo. 2014. Foraging activity rhythms of *Dinoponera quadriceps* (Hymenoptera: Formicidae) in

its natural environment. Journal of Insect Science 14:220.
Meinshausen, M., S. J. Smith, K. Calvin, J. S. Daniel, M. L. T. Kainuma, J.-F. Lamarque, K. Matsumoto, S. A. Montzka, S. C. B. Raper, K. Riahi, A. Thomson, G. J. M. Velders, and D. P. P. van Vuuren. 2011. The RCP greenhouse gas concentrations and their extensions from 1765 to 2300. Climatic Change 109:213–241.
Meyer, S. T., C. Koch, and W. W. Weisser. 2015. Towards a standardized rapid ecosystem function assessment (REFA). Trends in Ecology & Evolution 30:390–397.
Millien, V., S. Kathleen Lyons, L. Olson, F. A. Smith, A. B. Wilson, and Y. Yom-Tov. 2006. Ecotypic variation in the context of global climate change: revisiting the rules. Ecology Letters 9:853–869.
Mishra, M., and V. B. Meyer-Rochow. 2008. Eyes of male and female *Orgyia antiqua* (Lepidoptera; Lymantriidae) react differently to an exposure with UV-A. Micron 39:471–480.
Mittelbach, G. G., and D. W. Schemske. 2015. Ecological and evolutionary perspectives on community assembly. Trends in Ecology & Evolution 30:241–247.
Mlambo, M. C. 2014. Not all traits are "functional": insights from taxonomy and biodiversity-ecosystem functioning research. Biodiversity and Conservation 23:781–790.
Molleman, F., T. Remmel, and K. Sam. 2016. Phenology of predation on insects in a tropical forest: temporal variation in attack rate on dummy caterpillars. Biotropica 48:229–236.
Moretti, M., A. T. C. Dias, F. de Bello, F. Altermatt, S. L. Chown, F. M. Azcárate, J. R. Bell, B. Fournier, M. Hedde, J. Hortal, S. Ibanez, E. Öckinger, J. P. Sousa, J. Ellers, and M. P. Berg. 2017. Handbook of protocols for standardized measurement of terrestrial invertebrate functional traits. Functional Ecology 31:558–567.
Morley, R. J. 2003. Interplate dispersal paths for megathermal angiosperms. Perspectives in Plant Ecology, Evolution and Systematics 6:5–20.
Morley, R. J. 2011. Dispersal and paleoecology of tropical podocarps. Smithsonian Contributions to Botany 95:21–41.
Mouchet, M. A., S. Villéger, N. W. H. Mason, and D. Mouillot. 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. Functional Ecology 24:867–876.
Mouillot, D., D. R. Bellwood, C. Baraloto, J. Chave, R. Galzin, M. Harmelin-Vivien, M. Kulbicki, S. Lavergne, S. Lavorel, N. Mouquet, C. E. T. Paine, J. Renaud, and W. Thuiller. 2013. Rare species support vulnerable functions in high-diversity ecosystems. PLoS Biology 11:e1001569.
Mouquet, N., V. Devictor, C. N. Meynard, F. Munoz, L.-F. Bersier, J. Chave, P. Couteron, A. Dalecky, C. Fontaine, D. Gravel, O. J. Hardy, F. Jabot, S. Lavergne, M. Leibold, D. Mouillot, T. Münkemüller, S. Pavoine, A. Prinzing, A. S. L. Rodrigues, R. P. Rohr, E. Thébault, and W. Thuiller. 2012. Ecophylogenetics: advances and perspectives. Biological Reviews 87:769–785.
Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853–8.
Naeem, S., J. E. Duffy, and E. Zavaleta. 2012. The functions of biological diversity in an age of extinction. Science 336:1401–1406.
Nock, C. A., L. Baeten, A. Hector, K. Verheyen, W. W. Weisser, and M. Scherer-lorenzen. 2017. Quantifying relationships between biodiversity and ecosystem function with experiments. Pages 119–136*in* A. Chabbi and H. W. Loescher, editors.Terrestrial ecosystem research infrastructures: challenges and opportunities. CRC Press, Boca Raton, Florida, USA.
Nock, C. A., R. J. Vogt, and B. E. Beisner. 2016. Functional traits. Pages 1–8eLS. John Wiley & Sons, Chichester.
Noss, R. F. 1999. Assessing and monitoring forest biodiversity: a suggested framework and indicators. Forest Ecology and Management 115:135–146.
Nowrouzi, S., A. N. Andersen, S. Macfadyen, K. M. Staunton, J. VanDerWal, and S. K. A. Robson. 2016. Ant diversity and distribution along elevation gradients in the Australian wet tropics: the importance of seasonal moisture stability. PLOS ONE 11:e0153420.
O'Hara, R. B., and D. J. Kotze. 2010. Do not log-transform count data. Methods in Ecology and Evolution 1:118–122.
Ohlberger, J. 2013. Climate warming and ectotherm body size - from individual physiology to community ecology. Functional Ecology 27:991–1001.
Oindo, B. O. 2002. Patterns of herbivore species richness in Kenya and current ecoclimatic stability. Biodiversity and Conservation 11:1205–1221.
Oksanen, J., F. G. Blanchet, R. Kindt, P.

Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2016. vegan: community ecology package.

Olden, J. D., N. LeRoy Poff, M. R. Douglas, M. E. Douglas, and K. D. Fausch. 2004. Ecological and evolutionary consequences of biotic homogenization. Trends in Ecology & Evolution 19:18–24.

Oliver, T. H., M. S. Heard, N. J. B. Isaac, D. B. Roy, D. Procter, F. Eigenbrod, R. Freckleton, A. Hector, C. D. L. Orme, O. L. Petchey, V. Proença, D. Raffaelli, K. B. Suttle, G. M. Mace, B. Martín-López, B. A. Woodcock, and J. M. Bullock. 2015. Biodiversity and resilience of ecosystem functions. Trends in Ecology & Evolution 30:673–684.

Pace, M. L., J. J. Cole, S. R. Carpenter, and J. F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. Trends in Ecology & Evolution 14:483–488.

Pakeman, R. J., and H. M. Quested. 2007. Sampling plant functional traits: what proportion of the species need to be measured? Applied Vegetation Science 10:91–96.

Palmer, M. A., and C. M. Febria. 2012. The heartbeat of ecosystems. Science 336:1393–1394.

Paradis, E., J. Claude, and K. Strimmer. 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20:289–290.

Parr, C. L., P. Eggleton, A. B. Davies, T. A. Evans, and S. Holdsworth. 2016. Suppression of savanna ants alters invertebrate composition and influences key ecosystem processes. Ecology 97:1611–1617.

Parsons, S. M. A., and A. Joern. 2014. Life history traits associated with body size covary along a latitudinal gradient in a generalist grasshopper. Oecologia 174:379–91.

Pausas, J. G., and M. P. Austin. 2001. Patterns of plant species richness in relation to different environments: an appraisal. Journal of Vegetation Science 12:153–166.

Pavoine, S., and M. B. Bonsall. 2011. Measuring biodiversity to explain community assembly: a unified approach. Biological Reviews 86:792–812.

Peacor, S. D., and E. E. Werner. 2001. The contribution of trait-mediated indirect effects to the net effects of a predator. PNAS 98:3904–3908.

Pennington, R. T., M. Lavin, T. Särkinen, G. P. Lewis, B. B. Klitgaard, and C. E. Hughes. 2010. Contrasting plant diversification histories within the Andean biodiversity hotspot. Proceedings of the National Academy of Sciences of the United States of America 107:13783–13787.

Perkins, D. M., R. A. Bailey, M. Dossena, L. Gamfeldt, J. Reiss, M. Trimmer, and G. Woodward. 2015. Higher biodiversity is required to sustain multiple ecosystem processes across temperature regimes. Global Change Biology 21:396–406.

Petchey, O. L., and K. J. Gaston. 2002. Functional diversity (FD), species richness and community composition. Ecology Letters 5:402–411.

Petchey, O. L., and K. J. Gaston. 2006. Functional diversity: back to basics and looking forward. Ecology Letters 9:741–758.

Petchey, O. L., A. Hector, and K. J. Gaston. 2004. How do different measures of functional diversity perform? Ecology 85:847–857.

Peters, M. K., A. Mayr, J. Röder, N. J. Sanders, and I. Steffan-Dewenter. 2014a. Variation in nutrient use in ant assemblages along an extensive elevational gradient on Mt Kilimanjaro. Journal of Biogeography 41:2245–2255.

Peters, T., A. Braeuning, J. Muenchow, and M. Richter. 2014b. An ecological paradox: high species diversity and low position of the upper forest line in the Andean Depression. Ecology and Evolution 4:2134–2145.

Peters, T., T. Drobnik, H. Meyer, M. Rankl, M. Richter, R. Rollenbeck, B. Thies, and J. Bendix. 2013. Environmental changes affecting the Andes of Ecuador. Pages 19–29*in* J. Bendix, E. Beck, A. Bräuning, F. Makeschin, R. Mosandl, S. Scheu, and W. Wilcke, editors.Ecosystem services, biodiversity and environmental change in a tropical mountain ecosystem of South Ecuador. Springer, Berlin, Heidelberg.

Peters, V. E., K. U. Campbell, G. Dienno, M. García, E. Leak, C. Loyke, M. Ogle, B. Steinly, and T. O. Crist. 2016. Ants and plants as indicators of biodiversity, ecosystem services, and conservation value in constructed grasslands. Biodiversity and Conservation 25:1481–1501.

Peterson, A. T. 2011. Ecological niche conservatism: a time-structured review of evidence. Journal of Biogeography 38:817–827.

Philpott, S. M., I. Perfecto, I. Armbrecht, and C. L. Parr. 2010. Ant diversity and function in disturbed and changing habitats. Pages 137–156*in* L. Lach, C. L. Parr, and K. L.

Abbott, editors.Ant ecology. Oxford University Press.
Picaud, F., and D. P. Petit. 2007. Primary succession of Acrididae (Orthoptera): differences in displacement capacities in early and late colonizers of new habitats. Acta Oecologica 32:59–66.
Picaud, F., and D. P. Petit. 2008. Body size, sexual dimorphism and ecological succession in grasshoppers. Journal of Orthoptera Research 17:177–181.
Pickett, S. T. A. 1989. Space-for-time substitution as an alternative to long-term studies. Pages 110–135*in* G. E. Likens, editor.Long-term studies in ecology: approaches and alteratives. Springer, New York.
Pinto, R., V. N. de Jonge, and J. C. Marques. 2014. Linking biodiversity indicators, ecosystem functioning, provision of services and human well-being in estuarine systems: application of a conceptual framework. Ecological Indicators 36:644–655.
Van der Plas, F., T. M. Anderson, and H. Olff. 2012. Trait similarity patterns within grass and grasshopper communities: multitrophic community assembly at work. Ecology 93:836–846.
Pontarp, M., and J. J. Wiens. 2017. The origin of species richness patterns along environmental gradients: uniting explanations based on time, diversification rate and carrying capacity. Journal of Biogeography 44:722–735.
Poos, M. S., S. C. Walker, and D. A. Jackson. 2009. Functional-diversity indices can be driven by methodological choices and species richness. Ecology 90:341–347.
Prinzing, A., R. Reiffers, W. G. Braakhekke, S. M. Hennekens, O. Tackenberg, W. A. Ozinga, J. H. J. Schaminée, and J. M. van Groenendael. 2008. Less lineages - more trait variation: phylogenetically clustered plant communities are functionally more diverse. Ecology letters 11:809–19.
Prokopy, R. J. 1983. Visual detection of plants by herbivorous insects. Annual Review Entomol 28:337–364.
Qian, H. 2014. Contrasting relationships between clade age and temperature along latitudinal versus elevational gradients for woody angiosperms in forests of South America. Journal of Vegetation Science 25:1208–1215.
Qian, H., Z. Hao, and J. Zhang. 2014. Phylogenetic structure and phylogenetic diversity of angiosperm assemblages in forests along an elevational gradient in Changbaishan, China. Journal of Plant Ecology 7:154–165.
Qian, H., and R. E. Ricklefs. 2016. Out of the tropical lowlands: latitude versus elevation. Trends in Ecology & Evolution 31:738–741.
Qian, H., J. J. Wiens, J. Zhang, and Y. Zhang. 2015. Evolutionary and ecological causes of species richness patterns in North American angiosperm trees. Ecography 38:241–250.
Qian, H., Y. Zhang, J. Zhang, and X. Wang. 2013. Latitudinal gradients in phylogenetic relatedness of angiosperm trees in North America. Global Ecology and Biogeography 22:1183–1191.
Queathem, E. 1991. The ontogeny of grasshopper jumping performance. Journal of Insect Physiology 37:129–138.
De Queiroz, K. 2007. Species concepts and species delimitation. Systematic Biology 56:879–886.
R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for statistical computing. Vienna, Austria. URL http://R-project.org/.
Rahbek, C. 1995. The elevational gradient of species richness: a uniform pattern? Ecography 2:200–205.
Rahbek, C. 2005. The role of spatial scale and the perception of large-scale species-richness patterns. Ecology Letters 8:224–239.
Raimundo, R., A. Freitas, and P. Oliveira. 2009. Seasonal patterns in activity rhythm and foraging ecology in the Neotropical forest-dwelling ant, *Odontomachus chelifer* (Formicidae: Ponerinae). Annals of the Entomological Society of America 102:1151–1157.
Rangel, T. F., R. K. Colwell, G. R. Graves, K. Fučíková, C. Rahbek, and J. A. F. Diniz-Filho. 2015. Phylogenetic uncertainty revisited: implications for ecological analyses. Evolution 69:1301–1312.
Ratnasingham, S., and P. D. N. Hebert. 2007. BOLD: The barcode of life data system (http://www.barcodinglife.org). Molecular ecology notes 7:355–364.
Raven, P. H., and D. I. Axelrod. 1974. Angiosperm biogeography and past continental movements. Annals of the Missouri Botanical Garden 61:539–673.
Raymo, M. E., and W. F. Ruddiman. 1992. Tectonic forcing of late Cenozoic climate. Nature 359:117–122.
Read, J. L., and A. N. Andersen. 2000. The value of ants as early warning bioindicators: responses to pulsed cattle grazing at an

Australian arid zone locality. Journal of Arid Environments 45:231–251.
Reeves, J. L. 2011. Vision should not be overlooked as an important sensory modality for finding host plants. Environmental Entomology 40:855–863.
Revell, L. J. 2012. phytools: an R package for phylogenetic comparative biology (and other things). Methods in Ecology and Evolution 3:217–223.
Reymond, A., J. Purcell, D. Cherix, A. Guisan, and L. Pellissier. 2013. Functional diversity decreases with temperature in high elevation ant fauna. Ecological Entomology 38:364–373.
Ricklefs, R. E. 2004. A comprehensive framework for global patterns in biodiversity. Ecology Letters 7:1–15.
Ricklefs, R. E., and R. E. Latham. 1992. Intercontinental correlation of geographical ranges suggests stasis in ecological traits of relict genera of temperate perennial herbs. The American Naturalist 139:1305–1321.
Ricotta, C., M. Carboni, and A. T. R. Acosta. 2015. Let the concept of indicator species be functional! Journal of Vegetation Science 26:839–847.
Röder, J., F. Detsch, I. Otte, T. Appelhans, T. Nauss, M. K. Peters, and R. Brandl. 2017. Heterogeneous patterns of abundance of epigeic arthropod taxa along a major elevation gradient. Biotropica 49:217–228.
Roff, D. A. 1990. The evolution of flightlessness in insects. Ecological Monographs 60:389–421.
Rollenbeck, R., and J. Bendix. 2011. Rainfall distribution in the Andes of southern Ecuador derived from blending weather radar data and meteorological field observations. Atmospheric Research 99:277–289.
Romdal, T. S., M. B. Araújo, and C. Rahbek. 2013. Life on a tropical planet: niche conservatism and the global diversity gradient. Global Ecology and Biogeography 22:344–350.
Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. Nature 421:57–60.
Roslin, T., B. Hardwick, V. Novotny, W. K. Petry, N. R. Andrew, A. Asmus, I. C. Barrio, Y. Basset, A. L. Boesing, T. C. Bonebrake, E. K. Cameron, W. Dáttilo, D. A. Donoso, P. Drozd, C. L. Gray, D. S. Hik, S. J. Hill, T. Hopkins, S. Huang, B. Koane, B. Laird-Hopkins, L. Laukkanen, O. T. Lewis, S. Milne, I. Mwesige, A. Nakamura, C. S. Nell, E. Nichols, A. Prokurat, K. Sam, N. M. Schmidt, A. Slade, V. Slade, A. Suchanková, T. Teder, S. van Nouhuys, V. Vandvik, A. Weissflog, V. Zhukovich, and E. M. Slade. 2017. Higher predation risk for insect prey at low latitudes and elevations. Science 356:742–744.
De Ruiter, P. C., A. M. Neutel, and J. C. Moore. 1995. Energetics, patterns of interaction strengths, and stability in real ecosystems. Science 269:1257–1260.
Rutowski, R. L. 2000. Variation of eye size in butterflies: inter- and intraspecific patterns. Journal of Zoology 252:187–195.
Ryder Wilkie, K. T., A. L. Mertl, and J. F. A. Traniello. 2009. Diversity of ground-dwelling ants (Hymenoptera : Formicidae) in primary and secondary forests in Amazonian Ecuador. Myrmecol. News 12:139–147.
Salas-Lopez, A., H. Mickal, F. Menzel, and J. Orivel. 2017. Ant-mediated ecosystem processes are driven by trophic community structure but mainly by the environment. Oecologia 183:249–261.
Salazar, F., F. Reyes-Bueno, D. Sanmartin, and D. A. Donoso. 2015. Mapping continental Ecuadorian ant species. Sociobiology 62:132–162.
Sam, K., B. Koane, and V. Novotny. 2015a. Herbivore damage increases avian and ant predation of caterpillars on trees along a complete elevational forest gradient in Papua New Guinea. Ecography 38:293–300.
Sam, K., T. Remmel, and F. Molleman. 2015b. Material affects attack rates on dummy caterpillars in tropical forest where arthropod predators dominate: an experiment using clay and dough dummies with green colourants on various plant species. Entomologia Experimentalis et Applicata 157:317–324.
Sanders, N. J., J.-P. Lessard, M. C. Fitzpatrick, and R. R. Dunn. 2007. Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains. Global Ecology and Biogeography 16:640–649.
Sanders, N. J., J. Moss, and D. Wagner. 2003. Patterns of ant species richness along elevational gradients in an arid ecosystem. Global Ecology and Biogeography 12:93–102.
Schellenberger Costa, D., A. Classen, S. Ferger, M. Helbig-Bonitz, M. Peters, K. Böhning-Gaese, I. Steffan-Dewenter, and M. Kleyer. 2017. Relationships between abiotic

environment, plant functional traits, and animal body size at Mount Kilimanjaro, Tanzania. PloS one 12:e0174157.
Schleuning, M., J. Fründ, and D. García. 2015. Predicting ecosystem functions from biodiversity and mutualistic networks: an extension of trait-based concepts to plant-animal interactions. Ecography 38:380–392.
Schoereder, J. H., T. G. Sobrinho, C. R. Ribas, and R. B. F. Campos. 2004. Colonization and extinction of ant communities in a fragmented landscape. Austral Ecology 29:391–398.
Scholes, R. J., G. M. Mace, W. Turner, G. N. Geller, N. Jurgens, A. Larigauderie, D. Muchoney, B. A. Walther, and H. A. Mooney. 2008. Toward a global biodiversity observing system. Science 321:1044–1045.
Schwartz, M. W., C. A. Brigham, J. D. Hoeksema, K. G. Lyons, M. H. Mills, and P. J. van Mantgem. 2000. Linking biodiversity to ecosystem function: implications for conservation ecology. Oecologia 122:297–305.
Segovia, R. A., and J. J. Armesto. 2015. The Gondwanan legacy in South American biogeography. Journal of Biogeography 42:209–217.
Segovia, R. A., L. F. Hinojosa, M. F. Pérez, and B. a. Hawkins. 2013. Biogeographic anomalies in the species richness of Chilean forests: incorporating evolution into a climatic - historic scenario. Austral Ecology 38:905–914.
Seifert, C. L., C. H. Schulze, T. C. T. Dreschke, H. Frötscher, and K. Fiedler. 2016. Day vs. night predation on artificial caterpillars in primary rainforest habitats - an experimental approach. Entomologia Experimentalis et Applicata 158:54–59.
Seppelt, R., C. F. Dormann, F. V. Eppink, S. Lautenbach, and S. Schmidt. 2011. A quantitative review of ecosystem service studies: approaches, shortcomings and the road ahead. Journal of Applied Ecology 48:630–636.
Shelomi, M. 2012. Where are we now? Bergmann's rule sensu lato in insects. The American Naturalist 180:511–519.
Shingleton, A. W., W. A. Frankino, T. Flatt, H. F. Nijhout, and D. J. Emlen. 2007. Size and shape: the developmental regulation of static allometry in insects. BioEssays 29:536–548.
Shipley, B. 2009. Confirmatory path analysis in a generalized multilevel context. Ecology 90:363–368.
Siddig, A. A. H., A. M. Ellison, A. Ochs, C. Villar-Leeman, and M. K. Lau. 2016. How do ecologists select and use indicator species to monitor ecological change? Insights from 14 years of publication in Ecological Indicators. Ecological Indicators 60:223–230.
Slade, E. M., L. Kirwan, T. Bell, C. Philipson, O. T. Lewis, and T. Roslin. 2017. The importance of species identity and interactions on multifunctionality depends on how ecosystem functions are valued. Ecology in press.
Slik, J. W. F., N. Raes, S.-I. Aiba, F. Q. Brearley, C. H. Cannon, E. Meijaard, H. Nagamasu, R. Nilus, G. Paoli, A. D. Poulsen, D. Sheil, E. Suzuki, J. L. C. H. Van Valkenburg, C. O. Webb, P. Wilkie, and S. Wulffraat. 2009. Environmental correlates for tropical tree diversity and distribution patterns in Borneo. Diversity and Distributions 15:523–532.
Snyder, W. E., G. B. Snyder, D. L. Finke, and C. S. Straub. 2006. Predator biodiversity strengthens herbivore suppression. Ecology letters 9:789–96.
Soliveres, S., F. van der Plas, P. Manning, D. Prati, M. M. Gossner, S. C. Renner, F. Alt, H. Arndt, V. Baumgartner, J. Binkenstein, K. Birkhofer, S. Blaser, N. Blüthgen, S. Boch, S. Böhm, C. Börschig, F. Buscot, T. Diekötter, J. Heinze, N. Hölzel, K. Jung, V. H. Klaus, T. Kleinebecker, S. Klemmer, J. Krauss, M. Lange, E. K. Morris, J. Müller, Y. Oelmann, J. Overmann, E. Pašalić, M. C. Rillig, H. M. Schaefer, M. Schloter, B. Schmitt, I. Schöning, M. Schrumpf, J. Sikorski, S. A. Socher, E. F. Solly, I. Sonnemann, E. Sorkau, J. Steckel, I. Steffan-Dewenter, B. Stempfhuber, M. Tschapka, M. Türke, P. C. Venter, C. N. Weiner, W. W. Weisser, M. Werner, C. Westphal, W. Wilcke, V. Wolters, T. Wubet, S. Wurst, M. Fischer, and E. Allan. 2016. Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. Nature 536:456–459.
Sømme, L. 1989. Adaptations of terrestrial arthropods to the alpine environment. Biological Reviews 64:367–407.
Song, Y., P. Wang, G. Li, and D. Zhou. 2014. Relationships between functional diversity and ecosystem functioning: a review. Acta Ecologica Sinica 34:85–91.
La Sorte, F. A., S. H. M. Butchart, W. Jetz, and K. Böhning-Gaese. 2014. Range-wide latitudinal and elevational temperature gradients for the world's terrestrial birds: implications under global climate change.

PloS one 9:e98361.
Spasojevic, M. J., and K. N. Suding. 2012. Inferring community assembly mechanisms from functional diversity patterns: the importance of multiple assembly processes. Journal of Ecology 100:652–661.
Spehn, E. M., A. Hector, J. Joshi, M. Scherer-Lorenzen, B. Schmid, E. Bazeley-White, C. Beierkuhnlein, M. C. Caldeira, M. Diemer, P. G. Dimitrakopoulos, J. A. Finn, H. Freitas, P. S. Giller, J. Good, R. Harris, P. Högberg, K. Huss-Danell, A. Jumpponen, J. Koricheva, P. W. Leadley, M. Loreau, A. Minns, C. P. H. Mulder, G. O'Donovan, S. J. Otway, C. Palmborg, J. S. Pereira, A. B. Pfisterer, A. Prinz, D. J. Read, E.-D. Schulze, A.-S. D. Siamantziouras, A. C. Terry, A. Y. Troumbis, F. I. Woodward, S. Yachi, and J. H. Lawton. 2005. Ecosystem effects of biodiversity manipulations in European grasslands. Ecological Monographs 75:37–63.
Srivastava, D. S., M. W. Cadotte, A. A. M. Macdonald, R. G. Marushia, and N. Mirotchnick. 2012. Phylogenetic diversity and the functioning of ecosystems. Ecology Letters 15:637–648.
Stan Development Team. 2016. rstanarm: Bayesian applied regression modeling via Stan. R package version 2.13.1. http://mc-stan.org/.
Steiner, A. L. 1981. Anti-predator strategies. II. Grasshoppers (Orthoptera, Acrididae) attacked by *Prionyx parkeri* and some *Tachysphex* wasps (Hymenoptera, Sphecinae and Larrinae): a descriptive study. Psyche 88:1–24.
Stephens, P. R., and J. J. Wiens. 2003. Explaining species richness from continents to communities: the time-for-speciation effect in emydid turtles. The American naturalist 161:112–128.
Stern, D., and D. Emlen. 1999. The developmental basis for allometry in insects. Development 126:1091–1101.
Storch, D. 2003. Comment on "Global biodiversity, biochemical kinetics, and the energetic-equivalence rule." Science 299:346.
Stuart-Smith, R. D., A. E. Bates, J. S. Lefcheck, J. E. Duffy, S. C. Baker, R. J. Thomson, J. F. Stuart-Smith, N. A. Hill, S. J. Kininmonth, L. Airoldi, M. A. Becerro, S. J. Campbell, T. P. Dawson, S. A. Navarrete, G. A. Soler, E. M. A. Strain, T. J. Willis, and G. J. Edgar. 2013. Integrating abundance and functional traits reveals new global hotspots of fish diversity. Nature 501:539–42.
Sundqvist, M. K., N. J. Sanders, and D. a. Wardle. 2013. Community and ecosystem responses to elevational gradients: processes, mechanisms, and insights for global change. Annual Review of Ecology, Evolution, and Systematics 44:261–280.
Swenson, N. G. 2011. The role of evolutionary processes in producing biodiversity patterns, and the interrelationships between taxonomic, functional and phylogenetic biodiversity. American journal of botany 98:472–80.
Swenson, N. G., B. J. Enquist, J. Pither, J. Thompson, and J. K. Zimmerman. 2006. The problem and promise of scale dependency in community phylogenetics. Ecology 87:2418–2424.
Swenson, N. G., B. J. Enquist, J. Thompson, and J. K. Zimmerman. 2007. The influence of spatial and size scale on phylogenetic relatedness in tropical forest communities. Ecology 88:1770–1780.
Swenson, N. G., J. C. Stegen, S. J. Davies, D. L. Erickson, J. Forero-Montaña, A. H. Hurlbert, W. J. Kress, J. Thompson, M. Uriarte, S. J. Wright, and J. K. Zimmerman. 2012. Temporal turnover in the composition of tropical tree communities: Functional determinism and phylogenetic stochasticity. Ecology 93:490–499.
Swenson, N. G., and M. D. Weiser. 2010. Plant geography upon the basis of functional traits: an example from eastern North American trees. Ecology 91:2234–2241.
Tallents, L. A., J. C. Lovett, J. B. Hall, and A. C. Hamilton. 2005. Phylogenetic diversity of forest trees in the Usambara mountains of Tanzania: correlations with altitude. Botanical Journal of the Linnean Society 149:217–228.
Tang, C. Q., C. D. L. Orme, L. Bunnefeld, F. A. Jones, S. Powell, M. W. Chase, T. G. Barraclough, and V. Savolainen. 2016. Global monocot diversification: geography explains variation in species richness better than environment or biology. Botanical Journal of the Linnean Society 506:89–92.
The Angiosperm Phylogeny Group. 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. Botanical Journal of the Linnean Society 181:1–20.
Tilman, D., P. B. Reich, and F. Isbell. 2012. Biodiversity impacts ecosystem productivity as much as resources, disturbance, or herbivory. Proceedings of

the National Academy of Sciences of the United States of America 109:10394–7.
Tilman, D., P. B. Reich, and J. M. H. Knops. 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. Nature 441:629–632.
Del Toro, I., R. R. Silva, and A. M. Ellison. 2015. Predicted impacts of climatic change on ant functional diversity and distributions in eastern North American forests. Diversity and Distributions 21:781–791.
Tu, Y.-K., M. Kellett, V. Clerehugh, and M. S. Gilthorpe. 2005. Problems of correlations between explanatory variables in multiple regression analyses in the dental literature. British Dental Journal 199:457–461.
Underwood, E. C., and B. L. Fisher. 2006. The role of ants in conservation monitoring: if, when, and how. Biological Conservation 132:166–182.
Valencia, R., N. Pitman, S. León-Yánez, and P. M. Jorgensen. 2000. Libro rojo de las plantas endémicas del Ecuador 2000. Pontificia Universidad Católica del Ecuador, Quito.
Valiente-Banuet, A., M. A. Aizen, J. M. Alcántara, J. Arroyo, A. Cocucci, M. Galetti, M. B. García, D. García, J. M. Gómez, P. Jordano, R. Medel, L. Navarro, J. R. Obeso, R. Oviedo, N. Ramírez, P. J. Rey, A. Traveset, M. Verdú, and R. Zamora. 2015. Beyond species loss: the extinction of ecological interactions in a changing world. Functional Ecology 29:299–307.
Vandewalle, M., F. de Bello, M. P. Berg, T. Bolger, S. Dolédec, F. Dubs, C. K. Feld, R. Harrington, P. A. Harrison, S. Lavorel, P. M. da Silva, M. Moretti, J. Niemelä, P. Santos, T. Sattler, J. P. Sousa, M. T. Sykes, A. J. Vanbergen, and B. A. Woodcock. 2010. Functional traits as indicators of biodiversity response to land use changes across ecosystems and organisms. Biodiversity and Conservation 19:2921–2947.
Veach, V., E. Di Minin, F. M. Pouzols, and A. Moilanen. 2017. Species richness as criterion for global conservation area placement leads to large losses in coverage of biodiversity. Diversity and Distributions 23:715–726.
Venail, P., K. Gross, T. H. Oakley, A. Narwani, E. Allan, P. Flombaum, F. Isbell, J. Joshi, P. B. Reich, D. Tilman, J. van Ruijven, and B. J. Cardinale. 2015. Species richness, but not phylogenetic diversity, influences community biomass production and temporal stability in a re-examination of 16 grassland biodiversity studies. Functional Ecology 29:615–626.
Verheyen, K., M. Vanhellemont, H. Auge, L. Baeten, C. Baraloto, N. Barsoum, S. Bilodeau-Gauthier, H. Bruelheide, B. Castagneyrol, D. Godbold, J. Haase, A. Hector, H. Jactel, J. Koricheva, M. Loreau, S. Mereu, C. Messier, B. Muys, P. Nolet, A. Paquette, J. Parker, M. Perring, Q. Ponette, C. Potvin, P. Reich, A. Smith, M. Weih, and M. Scherer-Lorenzen. 2016. Contributions of a global network of tree diversity experiments to sustainable forest plantations. Ambio 45:29–41.
Villéger, S., N. W. H. Mason, and D. Mouillot. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89:2290–2301.
Violle, C., M.-L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel, and E. Garnier. 2007. Let the concept of trait be functional! Oikos 116:882–892.
Violle, C., P. B. Reich, S. W. Pacala, B. J. Enquist, and J. Kattge. 2014. The emergence and promise of functional biogeography. Proceedings of the National Academy of Sciences of the United States of America 111:13690–6.
Vogt, J. T., W. a. Smith, R. A. Grantham, and R. E. Wright. 2003. Effects of temperature and season on foraging activity of red imported fire ants (Hymenoptera: Formicidae) in Oklahoma. Environmental Entomology 32:447–451.
Wagemann, J., B. Thies, R. Rollenbeck, T. Peters, and J. Bendix. 2015. Regionalization of wind-speed data to analyse tree-line wind conditions in the eastern Andes of southern Ecuador. Erdkunde 69:3–19.
Wallace, A. R. 1878. Tropical nature, and other essays. Macmillan and Co., London.
Wallis, C. I. B., G. Brehm, D. A. Donoso, K. Fiedler, J. Homeier, D. Paulsch, D. Süßenbach, Y. Tiede, R. Brandl, N. Farwig, and J. Bendix. 2017. Remote sensing improves prediction of tropical montane species diversity but performance differs among taxa. Ecological Indicators.
Walters, M., and R. J. Scholes. 2017. The GEO handbook on biodiversity observation networks. Page (M. Walters and R. J. Scholes, Eds.). Springer International Publishing, Cham.
Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416:389–395.

Walther, G. R. 2010. Community and ecosystem responses to recent climate change. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2019–2024.

Warton, D. I., R. A. Duursma, D. S. Falster, and S. Taskinen. 2012. smatr 3 - an R package for estimation and inference about allometric lines. Methods in Ecology and Evolution 3:257–259.

Waters, C. N., J. Zalasiewicz, C. Summerhayes, A. D. Barnosky, C. Poirier, A. Gałuszka, A. Cearreta, M. Edgeworth, E. C. Ellis, M. Ellis, C. Jeandel, R. Leinfelder, J. R. McNeill, D. deB. Richter, W. Steffen, J. Syvitski, D. Vidas, M. Wagreich, M. Williams, A. Zhisheng, J. Grinevald, E. Odada, N. Oreskes, and A. P. Wolfe. 2016. The Anthropocene is functionally and stratigraphically distinct from the Holocene. Science 351.

Watt, C., S. Mitchell, and V. Salewski. 2010. Bergmann's rule; a concept cluster? Oikos 119:89–100.

Webb, C. O., D. D. Ackerly, and S. W. Kembel. 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. Bioinformatics 24:2098–100.

Webb, C. O., D. D. Ackerly, M. A. McPeek, and M. J. Donoghue. 2002. Phylogenies and community ecology. Annual Review of Ecology and Systematics 33:475–505.

Webb, C. T., J. A. Hoeting, G. M. Ames, M. I. Pyne, and N. LeRoy Poff. 2010. A structured and dynamic framework to advance traits-based theory and prediction in ecology. Ecology Letters 13:267–283.

Weiher, E., and P. A. Keddy. 1995. Assembly rules, null models, and trait dispersion: new questions from old patterns. Oikos 74:159.

Weiser, M. D., and M. Kaspari. 2006. Ecological morphospace of New World ants. Ecological Entomology 31:131–142.

Werner, F. A., and J. Homeier. 2015. Is tropical montane forest heterogeneity promoted by a resource-driven feedback cycle? Evidence from nutrient relations, herbivory and litter decomposition along a topographical gradient. Functional Ecology 29:430–440.

Whitman, D. W. 1987. Thermoregulation and daily activity patterns in a black desert grasshopper, *Taeniopoda eques*. Animal Behaviour 35:1814–1826.

Whitman, D. W. 2008. The significance of body size in the Orthoptera: a review. Journal of Orthoptera Research 17:117–134.

Wiens, J. J., D. D. Ackerly, A. P. Allen, B. L. Anacker, L. B. Buckley, H. V Cornell, E. I. Damschen, T. J. Davies, J.-A. Grytnes, S. P. Harrison, B. A. Hawkins, R. D. Holt, C. M. Mccain, and P. R. Stephens. 2010. Niche conservatism as an emerging principle in ecology and conservation biology. Ecology Letters 13:1310–24.

Wiens, J. J., and M. J. Donoghue. 2004. Historical biogeography, ecology and species richness. Trends in Ecology & Evolution 19:639–44.

Wiens, J. J., and C. H. Graham. 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. Annual Review of Ecology, Evolution, and Systematics 36:519–539.

Wiens, J. J., C. H. Graham, D. S. Moen, S. A. Smith, and T. W. Reeder. 2006. Evolutionary and ecological causes of the latitudinal diversity gradient in hylid frogs: treefrog trees unearth the roots of high tropical diversity. The American Naturalist 168:579–596.

Wiescher, P. T., J. M. C. Pearce-Duvet, and D. H. Feener. 2012. Assembling an ant community: species functional traits reflect environmental filtering. Oecologia 169:1063–1074.

Wilcke, W., Y. Oelmann, A. Schmitt, C. Valarezo, W. Zech, and J. Homeier. 2008. Soil properties and tree growth along an altitudinal transect in Ecuadorian tropical montane forest. Journal of Plant Nutrition and Soil Science 171:220–230.

Willig, M. R., D. M. Kaufman, and R. D. Stevens. 2003. Pattern, process, scale, and synthesis. Annual Review of Ecology, Evolution, and Systematics 34:273–309.

Winfree, R., J. W. Fox, N. M. Williams, J. R. Reilly, and D. P. Cariveau. 2015. Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. Ecology Letters 18:626–635.

Wohlgemuth, D., M. Solan, and J. A. Godbold. 2017. Species contributions to ecosystem process and function can be population dependent and modified by biotic and abiotic setting. Proceedings of the Royal Society of London B: Biological Sciences 284.

Wolf, K., E. Veldkamp, J. Homeier, and G. O. Martinson. 2011. Nitrogen availability links forest productivity, soil nitrous oxide and nitric oxide fluxes of a tropical montane forest in southern Ecuador. Global Biogeochemical Cycles 25:GB4009.

Wolverton, S., M. A. Huston, J. H. Kennedy, K.

Cagle, and J. D. Cornelius. 2009. Conformation to Bergmann's Rule in White-tailed Deer can be explained by food availability. The American Midland Naturalist 162:403–417.

Woodcock, P., D. P. Edwards, T. M. Fayle, R. J. Newton, C. V. Khen, S. H. Bottrell, and K. C. Hamer. 2011. The conservation value of South East Asia's highly degraded forests: evidence from leaf-litter ants. Philosophical Transactions of the Royal Society B: Biological Sciences 366:3256–3264.

Yanoviak, S. P., and M. Kaspari. 2000. Community structure and the habitat templet: ants in the tropical forest canopy and litter. Oikos 89:259–266.

Yasuhara, M., and R. Danovaro. 2016. Temperature impacts on deep-sea biodiversity. Biological Reviews 91:275–287.

Yates, M. L., N. R. Andrew, M. Binns, and H. Gibb. 2014. Morphological traits: predictable responses to macrohabitats across a 300 km scale. PeerJ 2:e271.

Yusah, K. M., and W. A. Foster. 2016. Tree size and habitat complexity affect ant communities (Hymenoptera: Formicidae) in the high canopy of Bornean rain forest. Myrmecol. News 23:15–23.

Zavaleta, E. S., J. R. Pasari, K. B. Hulvey, and G. D. Tilman. 2010. Sustaining multiple ecosystem functions in grassland communities requires higher biodiversity. Proceedings of the National Academy of Sciences of the United States of America 107:1443–6.

Zelený, D., and A. P. Schaffers. 2012. Too good to be true: pitfalls of using mean Ellenberg indicator values in vegetation analyses. Journal of Vegetation Science 23:419–431.

Zera, A. J., and R. F. Denno. 1997. Physiology and ecology of dispersal polymorphism in insects. Annual Review of Entomology 42:207–230.

Zeuss, D., S. Brunzel, and R. Brandl. 2017. Environmental drivers of voltinism and body size in insect assemblages across Europe. Global Ecology and Biogeography 26:154–165.

Zupan, L., M. Cabeza, L. Maiorano, C. Roquet, V. Devictor, S. Lavergne, D. Mouillot, N. Mouquet, J. Renaud, and W. Thuiller. 2014. Spatial mismatch of phylogenetic diversity across three vertebrate groups and protected areas in Europe. Diversity and Distributions 20:674–685.

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Curriculum vitae

Yvonne Christin Tiede - Curriculum vitae

Die Seite 139 (Lebenslauf) enthält persönliche Daten. Sie ist deshalb nicht Bestandteil der Online-Veröffentlichung.

Erklärung

Erklärung

Hiermit versichere ich, dass ich meine Dissertation mit dem Titel

„Multiple facets of biodiversity:
Assembly processes, trait composition, and functionality along tropical elevation gradients“

selbstständig und ohne unerlaubte Hilfe verfasst habe. Ich habe mich keiner als der in ihr angegebenen Quellen oder Hilfsmittel bedient und alle vollständig oder sinngemäß übernommenen Zitate als solche gekennzeichnet. Diese Dissertation wurde in der vorliegenden oder einer ihr ähnlichen Form noch bei keiner anderen in- oder ausländischen Hochschule eingereicht und hat noch keinen sonstigen Prüfungszwecken gedient.

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